Online Material Contents

Tables

Online Files for "Spider webs: behavior, function and evolution"

These online files complement the text in Chapters 2, 3, 6 and 9-10 in various ways. The numbers of the different sections here correspond to the chapter numbers in the book with an "O" added; table numbers are also coordinated with chapters (e.g., Table O2.1 complements topics discussed in chapter 2). Some sections focus largely on the limits of some previous studies: O3.1concerns the possible importance of orb visibility; O3.2 largely concerns difficulties in attempts to model orb web function. Tables O3.2– O3.5 constitute the most complete summary and critical evaluation of evidence concerning the controversial topic of the function(s) of silk stabilimenta yet compiled; they form the empirical basis for the discussion in section 3.3.4.

Sections O6.1 – O6.3 greatly extend the descriptions of construction behavior in Chapter 6. O6.1 provides additional details of the behavior of the two "focus" species, *Micrathena duodecimspinosa* and *Araneus diadematus*. O6.2, provides new, previously unpublished details of *M. duodecimspinosa* orb construction behavior. They are based on video recordings, and provide a finer level of detail than that available to date for any other species. And O6.3 adds observations of orb construction behavior of many other taxa. These sections open the door for detailed comparative studies of other species.

Sections O9.1- O9.3 present concrete examples of a major theme of Chapter 6, the tendency to converge on particular web designs in widely diverse taxa.

O3.1. The importance of orb visibility: critical comments

O3.1.1 Intrinsic visibility of an orb

There is little doubt that prey sometimes avoid orb webs that they have apparently perceived visually, at least in certain situations when there is no wind and webs are well illuminated and have simple visual backgrounds (section 3.3.3.2). Demonstrating that the degree to which an orb is visible affects prey capture under more natural conditions in the field is more complicated: the visibility of an orb is undoubtedly influenced by complex interactions among reflectance properties of silk lines, web architecture, ambient light, visual backgrounds, and insect visual capabilities, and avoidance by flight patterns and speeds in the field. This Appendix examines critically the evidence for some published conclusions regarding the importance of web visibility for selection on orb web designs.

Stingless bees learned to avoid more densely woven (and hence more visible) orbs more readily than less-dense orbs in field experiments, as expected (Craig 1994*a*). But the critical question for web evolution is not whether these bees are *capable* of learning, but whether learning in nature is frequent enough to affect selection on web visibility. Learning experiences may be so rare that spider feeding rates are not be affected significantly. This appeared to be the case in this experiment: at the start of these and other training experiments in the field (Craig et al. 1996) the bees showed that in fact they had *not* learned to avoid denser orb webs. Nor did they innately avoid them, at least under the conditions of the experiments (which were not entirely natural). The sample was relatively small, so conclusions can only be tentative, but available evidence suggests that these prey do not show greater avoidance of more densely woven webs in nature.

A second type of experimental test of the importance of visibility in the field involved experiments in which the visibility of orbs was manipulated by coating one half of each of a series of orbs of five species of araneids with corn starch mixed with powdered sugar (Craig 1988; Craig and Freeman 1991), and then counting the damaged sites where insects had collided with the web and struggled free. The coating was presumed to not affect the tendency of the web to be damaged when there was an impact by prey or detritus. In all species, the powdered portions accumulated fewer damaged sites that were attributed to prey impacts (Craig 1988; Craig and Freeman 1991). Extraordinarily, reductions in prey impacts occurred even occurred at night on powdered webs of the non-forest spider *Eustala* sp. when the moon was full, but not in *Eustala* sp. on nights when there was no moon (but not the forest species *Verrucosa* sp.) (Craig and Freeman 1991). This finding in nocturnal webs is so unexpected that it is worth examining these studies more carefully.

The technique of counting damaged sectors has several serious problems. The counts were not made blindly with respect to the treatment. This detail could be important, because evaluation of the number of impacts from web damage is not easy, and no definitions were given regarding the minimum alteration that was counted as prey or detritus damage. For example, I am unable to deduce the numbers of prey that collided with the orbs in Figs. 1.4, 3.5, 3.35, 4.3, or 4.15, even though these are all photos of fresh, relatively undamaged webs in which damage is less extensive and thus easier to characterize (the reader is invited to try to count prey impacts in these webs, and in those of Figs. 3.19 and 4.5 of more extensively damaged field webs). Counts are further complicated by the fact that single prey sometimes works only partly free in a vertical orb, and falls into another sector below ("tumbling" – see sections 3.3.3.1, 4.8, Fig. 4.20). Direct observations of tumbling insects showed that they produced trails of damaged sectors, some of which were obviously connected with each other, but others that lacked obvious connections (WE). Difficulty in distinguishing impacts could lead to inadvertent, unconscious bias in counts of damage on powdered and unpowdered areas of webs, because data were not taken blind. In addition, tumbling may have been less likely in coated webs (which presumably adhered less strongly to prey; the claim that adding powdered sugar compensated for this was not substantiated with data).

Still another problem with the "count the damage" technique is that the degree to which a coating of cornstarch and powdered sugar increases the visibility of an orb in the field, at least to the human eye, is far greater than the degree to which an increase in the densities of sticky spiral or radial lines affects the visibility of a normal, intact orb. It is possible that within the range of visibility of silk lines in normal orbs (especially in the case of nocturnal orbs), all lines are effectively invisible to most insect prey in the field; visually guided avoidance of powdered orbs may be irrelevant with respect to normal uncoated orbs in nature. Further problems with this powdering technique include possible inequalities in the sizes of the areas covered with powder, and possible variation in their exposure to insect flight paths or falling detritus (see Fig. 4.7A in Craig and Lehrer 2003*a*). There were no controls for the possibility of chemical attraction to or repulsion by corn starch and powdered sugar.

Still another problem with the biological relevance of some data is that the damage in these studies was quantified in terms of prey numbers, rather than prey mass; it thus failed to discriminate large from small, possibly trivial nutritional payoffs (section 4.2). Some other experimental studies regarding web visibility suffered from this prey size problem. For instance, the reactions of *Drosophila* flies to webs of adult female *Nephila* (e.g. Craig 1990) involve very minor payoffs to this large spider.

In sum, conclusions regarding natural selection on orb web visibility that were based on measurements using the technique of web powdering to alter web visibility and then counting areas damaged by prey are open to serious doubt.

O3.1.2 Effects of visual background

The poor vision of orb weavers and their tendency to build webs in the dark make it unlikely that during website choice a spider can make useful evaluations of the backgrounds against which prey will see her orb. Nevertheless, a general tendency to build in dimly illuminated sites could reduce selection on webs to reduce their visibility (Craig 1986). At least at a very superficial level, however, I do not see obvious patterns in general designs of species that built at protected websites (e.g., *Meta* and *Azilia*), compared with exposed orbs (e.g. the tetragnathids *Leucauge* spp. and *Tetragnatha* spp.), or that built nocturnal vs. diurnal orbs. But careful analyses are lacking, and there are many other possibly important variables; further study could be rewarding.

Testing ideas regarding backgrounds is difficult, because it is not easy to typify the backgrounds that prey see in nature. Take for example the basic idea that the more similar the spectral reflection of the silk is to that of the background, it may be more difficult it will be for prey to see. For instance, the yellow color of *N. clavipes* would result in high contrast when the web is viewed looking upward against a blue sky, but low contrast when viewed from the side against a background of vegetation (Craig and Lehrer 2003*b*). The orientation of prey as they fly into *Nephila* webs has not been checked, though more nearly horizontal flight paths (in which the visual background would be vegetation) would seem more likely than mainly upward paths. A prey approaching the lower side of a slanting web while flying horizontally would look more upward to see the web. The wide range of settings of *Nephila* webs, from deep in forests to completely exposed, makes it difficult to even speculate about the typical visual backgrounds perceived by prey. Another species with yellow webs, *Araneus expletus* (AR), are built close to vegetation in shaded but not dark second growth sites (WE).

Summing up, there is little doubt that some insects can see some spider webs in some situations, and it is feasible that that a web's visibility could influence its ability to capture prey. But moving from a theoretical possibility to a demonstrated effect in nature is difficult, and several of the techniques that have been employed to have serious limitations. The upshot is that there are strong hints that web visibility can be important, but the data assembled to demonstrate its importance are not convincing. Clearly the topic of the effects of web visibility in the field merits further study.

O3.1.3 UV reflectance of stabilimenta

The discovery that stabilimentum (aciniform) silk reflects light strongly in the UV (Craig and Bernard 1990), in combination with the fact that insects perceive UV wavelengths, provoked extensive research on the reflectance of different types of silk. Determining the implications of these studies for hypotheses regarding stabilimentum function is complex.

One hypothesis is that the strong UV reflectance of stabilimentum silk serves to attract prey to orb webs (e.g., Craig and Bernard 1990; Zschokke 2002). There are UV receptors in the eyes of most insects (Briscoe and Chittka 2001), and UV has long been known to attract insects in several contexts. Many are attracted at night (e.g. Mazokhin-Porshnyakov 1969; Barghini and Souza de Medeiros 2012), but this effect may be irrelevant to understanding the function of stabilimenta, which are built exclusively on orbs that are operated during the day (Table O3.3). The classic studies of diurnal UV attraction involved insects escaping from confinement. When, for instance, *Drosophila melanogaster* flies were jarred into the bottom of a Y maze or placed in a dark box with two windows, they tended to choose the arm or window which had UV light over an alternative arm or window that lacked UV (Mazokhin-Porshnyakov 1969; Hu and Stark 1977). These experiments demonstrated that they perceive UV, and are attracted when they are attempting to escape confinement; but they do not necessarily provide useful information on how potential insect prey behave while foraging undisturbed in nature.

Take, for instance, attempts to extend this type of data to conclude that insects use UV from the sun and the sky to locate open spaces: "… when insects fly from the interior of vegetation towards open space, they seek a UV-bright light gap … Silks suspended across vegetation gaps may attract prey by scattering both sunlight and sky light, making the gap appear bright in the UV region…" (Craig and Bernard 1990; p.616; see also Craig 2003). Perhaps such responses to UV occur when an insect is changing the patch in which it is foraging, or when it has been frightened and is attempting to escape; but they surely constitute only a portion (possibly quite small) of its time, compared with the time dedicated to other flight activities (e.g., long distance travel, searching visually for nearby resources, following odor plumes to find mates or food, etc.). How large is this fraction? What portion of the prey that are captured by orb weavers were engaged in escape behavior when they encountered the web? And how likely is a prey species to confuse a patch of silk on a spider web with a gap in the vegetation? How, in fact, does one test the hypothesis that when a foraging insect in the field flies up out of a patch of vegetation it shifts to using UV as an attractive cue, in addition to or rather than other wavelengths or gravity?

Another weakness of arguments based simply on the ability to perceive particular stimuli is that they do not take into account further processing in the animal's nervous system; the physiological capabilities of an animal's sense organs are not necessarily reflected directly in its behavior. Take for instance, the stabilimenta of *Argiope trifasciata* (AR) (McCook 1889) and the honeybee *Apis mellifera*. The combination of the high sensitivity of insect eyes to UV, the high UV reflectance of stabimentum silk, and the generally low UV reflectance of foliage (Craig 2003) probably makes the stabilimenta of *A. trifasciata* stand out clearly from the visual background for these bees (as well as for many other insects). A test by Blackledge and Wenzel (2000) of how *A. mellifera* bees use of these stabilimenta for orientation found a surprising result, however. When Blackledge and Wenzel studied the ability of free-ranging foraging bees to learn to use the presence or absence of different types of silk (which had different reflectances) as cues signaling the presence of food, they found that bees were less rather than more able to learn when the food source was marked with stabilimentum silk. So, paradoxically, the high UV (and blue and green) reflectance of the *A. trifasciata* stabilimenta apparently resulted in the bees using the stabilimentum silk less rather than more. Perhaps it was not a question of *seeing* the silk, but of avoiding it after seeing it? Whether these visual biases of *A. mellifera* are representative of those of other prey species native to habitats of *A. aurantia* is not known, but at least some insect species differ in this respect: one study that utilized artificial traps with and without zig-zag stabilimenta concluded that at least some orthopterans are not attracted to them (Tso 1998*a*).

In sum, high visibility is not equal to high attractiveness. This is no surprise, as animals often ignore some stimuli that they are physiologically capable of perceiving when they make decisions (e.g., the "sign stimuli" of classic ethology) (Robinson 1969).

A further question is whether or not the geometric patterns or designs in which the stabilimenta silk is placed on webs are in and of themselves attractive. This question is related to the third behavioral context in which UV has been argued to play a role in attracting prey: attraction of flower-visiting insects (Craig and Bernard 1990; Craig 2003). It is well-established that some insects use UV-reflecting "nectar guides" on flowers to guide them when they are near a flower (Wehner 1981). Again, however, applying evidence of this type of attraction to the possible function of UV-reflective stabilimenta is difficult.

In the first place, UV markings on flowers function to guide pollinators to the flower's nectar, but these guides include both UV-bright and UV-dark patterns (e.g., Barth 1985); UV reflectance *per se* is not necessarily attractive. Secondly, stabilimenta could only be expected to function as sensory traps for the subset of flying insect prey that are attracted visually to flowers (e.g., bees, some flies, some butterflies, a few beetles). Is there any evidence that the prey captured by spiders with silk stabilimenta are biased toward flower-visiting prey compared with webs in the same habitat that lack stabilimenta? There are several studies of the prey of orb weavers with and without stabilimenta (see Robinson and Robinson 1970*a* on *Argiope argentata*, Blackledge and Wenzel 1999 on *A. aurantia*, Cheng and Tso 2007 on *A. aemula*), but I know of no report of such a bias. In *A. aurantia* apid bees were equally commonly captured by webs with and without stabilimenta (38.0% of a total of 162 prey and 34.5% of 107 prey respectively) (Blackledge and Wenzel 1999). In further disagreement with the flower mimicry hypothesis, odonates, and insect group that does not visit flowers, constituted more than half (65%) of the large, wrapped prey captured by large immatures of *A. aurantia* at one site, and 49% of a mix of nymphs and adults at other sites (Howell and Ellender 1984). At still another site, grasshoppers, which seldom visit flowers, were a dominant large prey (Brown 1981).

I recognize that perhaps no one has ever checked specifically for a bias toward flower-visiting insects in the prey captured by orbs with stabilimenta (see however Craig and Ebert 1994 on the body coloration of *Argiope argentata*); and in any case, there are serious problems in making biologically realistic comparisons between web captures and "available" prey, and in choosing appropriate habitats in which to make the measurements (sections 3.2.5.6, O3.2.3), so interpreting such data is difficult. The point remains, however, that many of the prey (both in terms of numbers and mass) that are captured by some stabilimentum-building *Argiope* species are not species that typically visit flowers (e.g. odonates, grasshoppers) (Eberhard 1990*b*). Similarly, in a population of *Octonoba sybotides* (UL) in which 90.1% of the webs had stabilimenta, 82% of the prey were dipterans, many of which belonged to groups that are not strongly associated with flowers (39% were midges, 7% mosquitoes), and two of the other three orders that were captured (Ephemeroptera and Neuroptera) are also not typically associated with flowers (Watanabe 1999b). The patterns of silk stabimenta vary substantially, even within a species, from single lines, to zig-zag lines, to "X" forms to ovals, circles, and many other combinations (Fig. 3.40, Hingston 1932; Herberstein et al. 2000b). In sum, the attractiveness of these patterns themselves for insect prey and predators remains to be demonstrated in the field. On the other hand, various patterns appear designed to mimic or merge with the outlines of the spider (Figs. 3.40, 3.41, Hingston 1932).

Thirdly, many stabilimenta are inappropriately placed on the orb to trap insects that might be using their geometric patterns as nectar guides. For instance, the classic "X" of *Argiope* species is not centered on sticky lines that could trap prey that were guided to the intersection of the arms (Figs. 3.47), but rather on the non-sticky hub lines (where, of course, the spider rests).

The sites where some other stabilimentum-building species build their webs also argue against the flower-mimic hypothesis. Some build stabilimenta at sites where flowers are rare or completely absent, and where flower-visiting insects probably seldom visit. Examples include piles of dead branches and other plant debris on the ground (packrat nests) in a desert (*Uloborus diversus* – Eberhard 1971*a*); detritus near the floor of tropical forests (*Philoponella heredia* – Opell 1987); the tangles of silk lines above the funnel webs of the tengellid *Tengella radiata* that are built near tree trunks deep in tropical forests (*P. vicina* – Fincke 1981); among rocks and the roots of trees (*Octonoba sybotides* – Watanabe 1999b); high above tropical rivers (*Caerostris darwini* – Gregorič et al. 2011a,b); and on bare, dead twigs (*Polenecia producta* – Peters 1995).

The relative importance of different factors probably varies over time as well as space. As a spider grows during ontogeny, the payoff for a given stabilimentum design could vary substantially (e.g. Robinson and Robinson 1973*b*). Both the prey and the predators most important for small spiderlings undoubtedly differ from those that are most important for adults (section 3.2.5.5). Even for a single predator capable of preying on multiple sizes of spiders, stabilimentum function might differ. For instance, the visual extension of an individual *Argiope argentata*'s legs provided by its stabilimentum may inhibit attacks by gape-limited lizards when the spider is moderately large, but not when she is smaller (Schoener and Spiller 1992). Another complicating factor would be year to year variations. An individual's reproduction may be limited more by defense against predation in a year with abundant prey, or in a habitat (or a season or a year) in which predators are more abundant or have fewer alternative prey. The common finding that stabilimentum patterns also vary ontogenetically in form and frequency (e.g., Marples 1962; Ewer 1972; Lubin 1975, 1986; Robinson and Robinson 1978; Nentwig and Rogg 1988; Seah and Li

2002; Eberhard 2003; Rao et al. 2007; Uhl 2008) suggests that these balances may differ for individuals of the same species that have different sizes, or during different times of the year. Furthermore, there may even be individual variation in the ontogenetic timing of changes in stabilimenta (Ewer 1972).

In sum, the balances between costs and benefits probably vary in complex ways. Perhaps these complexities explain observations show contradictory results (#36-45 in Table O3.3). I do not have a final answer to the difficult question of whether or not the UV reflectance of stabilimentum silk makes stabilimenta attractive for insects in the field (see section 3.3.4.2, Tables O3.3 – O3.5). It is clear however that there are good reasons to question the assumption that the high UV reflectance of stabilimentum silk makes stabilimenta attractive to prey in the field. Without further data, simple declarations that UV light reflected from stabilimenta in the field is attractive to insect prey (e.g., Craig 2003) are open to serious doubt.

O3.1.4 Evolutionary origins versus maintenance

Most discussions of stabilimentum functions do not discriminate between natural selection on stabilimenta when they originally appeared as variations within a population, versus selection which subsequently maintained stabilimenta after they became established. Walter and Edgar (2012) argued that the prey attraction hypotheses discussed above cannot explain stabilimentum origins or why ancestral spiders first started to deposit silk on their webs, noting that there is no obvious component of the web-building process that may have led directly to the addition of web decorations. This is not quite true, however, as there are white masses of loose silk produced during radius construction in araneids and tetragnathids (for example, Figs. 4.17, 6.16, 7.6, 7.30, O6.4). In addition, part of this mass sometimes remains even after the hub center is removed (see Figs. 3.30 of *Leucauge mariana* TET and 3.37h of *Micrathena duodecimspinosa* AR).

Be that as it may, the argument of Walter and Edgar (2012) (characterized as the “silk reserve hypothesis” in Table O3.7) is that building a stabilimentum originated as a mechanism to activate the aciniform glands whose silk is used to wrap prey. Theyposit that the aciniform glands become activated from wrapping prey, and that this could lead to greater aciniform silk deposition when they rebuild webs, producing larger decorations. In turn, they argue, greater web-decorating activities while building a new web in the morning also activates the aciniform glands, providing the spider with larger quantities of wrapping silk for future prey-capture events. But both the metabolic costs and the delays involved in reingesting stabilimentum silk, breaking it down, and then resynthesizing it (the efficiency of recycling silk, at least drag line silk, is on the order of only 30% - Tillinghast and Townley 1987) could be avoided by simply refraining from adding a stabilimentum to the web; an alternative, more efficient mechanism to provide silk needed to wrap prey would be to simply increase aciniform gland production without using the silk for stabilimenta. In sum, I find these arguments unconvincing, and believe that the hypotheses discussed in the text and Tables O3.3-O3.5 are sufficient to explain even the original advantage conferred by the inclusion of wrapping silk at or near the hub.

O3.2 Difficulties in modeling orb web performance

The apparent ease with which the effects of differences in orb web geometry on prey capture can be estimated has led to repeated attempts to model orb web performance (e.g., Eberhard 1986*a*; Evans 2013). I will argue here, however, that this simplicity is an illusion. The following gives a preliminary illustration of some of the types of difficultie. Because a spider has only finite silk resources available, a reduction in the diameters of lines will enable her to make a less easily visible and larger web that intercepts more prey; but this web will also be less able to stop and retain prey, and less resistant to damage from wind and falling detritus. The balances between the gains and losses from thinner lines are likely to vary greatly for different types of prey. For instance, an improvement in the retention function could result in the capture some vigorous, heavy prey that are clumsy fliers and cannot avoid webs, but at the same time reduce captures of agile prey species that fly slowly or that can see and avoid webs. Not all prey are equally valuable to spiders: in general larger prey will provide more food and thus be proportionately more important, but they also tend to be rarer (), some may have noxious substances that reduce or even eliminate their nutritional value (Different effects on different prey must thus be weighted, according to the abundance of the prey in the natural habitats of the spider and their likelihood of becoming entangled in webs there, not an easy task.

I will first discuss models concerning the consquences of specific design properties, such as the spaces between sticky lines, and then those concerned with decisions regarding the total amounts of investment made in foraging. I believe that a major problem has been overly typological analyses.

O3.2.1 Variation I: “The” mesh size

Researchers (for example, Endo 1988; Schneider and Vollrath 1998; Blackledge and Eliason 2007; Herberstein and Tso 2000; Blackledge et al. 2011; Sensenig et al. 2010) have often characterized orbs with respect to “the mesh size” – the mean space between sticky lines. There are even formulae for calculating “the” value for an orb (e. g., Herberstein and Tso 2000). This usage is misleading in two respects. In common parlance, the mesh of a woven structure refers to the distances between lines in both the warp and the woof. But neither the distances between radii nor those between sticky spiral lines are constant in orbs (Zschokke 2002; Eberhard 2014; section 4.3). Radii are closer near the hub than at the edge of the orb, and the spaces between sticky spiral loops also commonly vary, often in stereotyped and sometimes complex ways.

Some simulation studies of the prey stopping function have simply ignored this variation by launching prey into “the middle of the capture areas” (Sensenig et al. 2012, p. 1882; judging by their Fig. 3, there was in fact substantial variation in where the simulated prey struck webs). But the consistencies in these patterns (even in horizontal orbs), along with intra-web and inter-specific variations in these patterns, argues that the spaces between loops are selectively important for orb weavers, and thus that it may be counterproductive to typify them with single values.

A second complication is that when a prey strikes an orb at a glancing angle (other than 90º), it will experience reduced distances between web lines (Fig. 3.23). For instance, a prey moving horizontally that makes a glancing impact in the capture area directly above or below the hub of a vertical orb will encounter more radii (and thus have a greater likelihood of being stopped) than if it made a similar impact in the capture area of the same orb to the side of the hub. An orb design with an elongate capture zone below the hub will increase the fraction of such glancing impacts in which the "effective" separation between radii is reduced, thus increasing the orb's ability to capture stop such prey. If, on the other hand, prey trajectories are often upward or downward rather than horizontal (as they seem to be in at least some sites – section 3.2.4), then the mean effective distance between radii (and the stopping function) in these areas will not be reduced. The relative sizes of different portions of the capture area and the trajectories of prey will determine the relative importances of these effects. All of this variation is ignored, without taking into account possible differences in importance, by assuming a single "mesh size".

Another generally ignored complication related to the separation between lines is that the ability of an orb to stop and retain prey, as well as its visibility to approaching prey, are surely influenced by the angle of the prey's trajectory with respect to the plane of the orb (Eberhard 1986*a*; Craig 2003). Most discussions consider only perpendicular impacts (e.g., Eberhard 1986*a*; Sensenig et al. 2012). Perpendicular impacts (which result in maximum effective separation between lines for the interception and stopping functions) may well be the exception rather than the rule, except when orbs are positioned against flat surfaces (e.g. the elongate tree trunk orbs) that probably cause prey to strike these orbs more nearly perpendicularly.

Further complexities may be introduced if spiders consistently position their orbs with respect to likely prey trajectories, or place them so that the peripheral rather than the more central regions (or vice versa) are more likely to intercept prey flight trajectories (e.g., the upper portions of *Gea heptagon* webs in Fig. 4.2). Ecologically realistic contexts in which such biases might occur include tilting the orb with respect to gravity, consistently orienting the web at some angle with respect to the direction of prevailing air currents, and siting the lower portion of the orb closer to the surface of water (Buskirk 1975) or some other substrate where prey densities are higher.

In sum, the functional characteristics of an orb web are not appropriately characterized by positing that it has any particular mesh size. This variation in the effective distances between lines can introduce noise, if not confusion, in modeling attempts that do not take it into account appropriately.

O3.2.2: "The" properties of silk lines

Models of both prey capture (to name a few, Eberhard 1986*a*; Sherman 1994; Herberstein and Heiling 1999; Craig 2003; Blackledge et al. 2009; Sensenig et al. 2010) and of web stability (e.g. Aoyanagi and Okumura 2010; Cranford et al. 2012) typically assume that the properties of homologous silk lines are uniform throughout an orb, and in orbs of different designs. This supposition was a reasonable first step, but recent studies have showed that some properties sometimes vary substantially in both non-sticky and (perhaps especially) sticky lines, even within a single web (section 3.2.9. In addition, environmental variables such as relative humidity can affect crucial mechanical properties such as extensibility and stickiness, and these effects are not necessarily the same for different species (Sensenig et al. 2010; Opell et al. 2013; Amarpuri et al. 2015). In the best case, variations in the mechanical properties of lines will represent "noise" in models that fail to take them into account. In the worst case, variations in properties may correlate with particular design properties of orbs, and lead to mistaken conclusions from models. Data on the mechanical properties of the lines of a variety of orb weavers that build different orb designs will be needed (for important starts in this direction, see Cartan and Miyashita 2000 and Sensenig et al. 2010).

An additional complication is that even lines with uniform properties may interact in different ways with different prey species. For instance, the strength of adhesion of uloborid sticky spiral lines varied among five different prey, and was affected by the size, type, and density of the insect's setae (Opell 1994; Opell and Schwend 2007). The setae on an insect's body are usually not uniform, and surely not equally exposed to contact with web lines when the insect strikes an orb, so there is probably further, intra-specific variation in the forces of adhesion.

O3.2.3 Variation III: The "available" prey

To determine an orb's functionality, it is crucial to knowthe sizes and types of prey that are available in a spider's habitat. At first glance, it would seem to be relatively simple to make accurate counts of the airborne prey. Indeed, estimates of this sort for web spiders are probably often simpler to perform and more precise than analogous counts of potential prey for other predators such as birds, lizards, and jumping spiders, because they have difficult-to-measure searching and attack biases, and prey that can hide and/or take evasive actions. The hope of obtaining good estimates of prey available for orb weavers in nature has spawned a large literature on the prey available to orb web spiders in nature. I believe, however, that there are several serious problems; prey vary in several important ways that can affect the likelihood that they will be captured by an orb weaver (see Turnbull 1960 for a clear summary).

The first difficulty is that simple counts of prey in the spiders' environment (e.g., Uetz and Biere 1980; Castillo and Eberhard 1983) are not sufficient to determine their relative importance as food. Prey that are present can differ substantially with respect to their likelihood of being captured. The likelihood of a prey being captured can be influenced by its surface area (especially the area likely to impact a web – the area perpendicular to the direction in which the prey flies), the strength with which sticky lines adhere to its body surface, its weight and speed of flight (momentum), its visual acuity (and thus its ability to see webs before impact), its agility and speed in flight (and thus its ability to avoid webs) (Fig. 3.2), the microhabitats and times of day in which it is active, and its common flight trajectories. Prey densities may vary even across a single orb, as illustrated by greater interception rates for orthopterans in the lower compared with the upper halves of *Argiope trifasciata* (AR) orbs (Tso 1996). And, of course, several of these traits also vary even for a given prey individual at different moments in its life (e.g. Craig 2003). On top of this, spider attack behavior varied strongly both between prey and between spider species (e.g. Robinson

1969; Robinson and Robinson 1976; Viera 1995), contributing further uncertainty to determining payoffs for spiders. In sum, being present in a habitat is definitely not equivalent to being available to an orb weaver.

One unsatisfactory “solution” to the problem of differences in susceptibility to being captured by orbs has been to count prey that accumulate in webs and are unable to escape over time (e.g., Endo 1988). This technique, however, focuses on precisely the prey that are least likely to be biologically important – the prey that are so weak and small that they cannot work free from the web and that the spider did not find important enough to attack. Experimental studies in which orbs or portions of orbs were mounted (without the spider) on artificial supports and then checked later for prey that they retained (Miyashita and Shinkai 1995; Opell et al. 2006) suffered from a similar problem. This technique is powerful in allowing fine control and replication with respect to the habitat in which the web is placed, but only counts relatively small and weak prey.

Another, more common but also unsatisfactory solution has been to count insects captured in artificial traps that are placed in the general habitat in which an orb weaving species occurs. Often these traps consist of sticky planar surfaces (e.g., Castillo and Eberhard 1983; Nentwig 1983; Shelly 1983, 1984; Rypstra 1985; Sherman 1994; Herberstein & Elgar 1994; Harwood et al. 2001; Hénaut et al. 2010). Other techniques employed flight intercept traps that collected the insects which fell downward after they encountered a transparent sheet (Edwards et al. 2009), or that flew upward into a trapping device (a Malaise trap) (Ludy 2007). In most cases there was little or no attempt to adjust the possibly important details of the sticky traps, such as the subhabitats where they were placed, the time of day when they were set out, their height above the ground, the size of open space where the trap was placed, the orientation of the trap with respect to air flow and gravity, the intrinsic visibility of the trap, the visual contrast of the trap with nearby objects, and degree of adhesiveness, in order to mimic spider webs. Many studies simply ignored most of these variables (I do not know of a single study that has attempted to mimic them all) (see Eberhard 1990*b* for a long, though now out of date list of such studies; unfortunately they have continued to accumulate).

These traps are also likely to give unsatisfactory data on prey capture by orbs, for several other reasons. The sticky lines of the traps are unbreakable for even the heaviest, fastest moving prey (Castillo and Eberhard 1983; Nentwig 1983), and can thus mimic interception but not stopping and retention of prey. The abilities of different prey to struggle free will differ in orbs compared with traps. Different prey will have different abilities to escape the spider’s attack, through resistance to adhesion, “playing dead” behavior) (Suter 1978; section 4.11), and through active spider rejection of some prey in favor of others (Eisner and Dean 1976; Robinson and Olazarri 1971; Castillo and Eberhard 1983). In some cases rejection is complex, as it is based on previous learning (Turnbull 1960). In sum, there are multiple theoretical reasons to suspect that artificial traps will not provide even moderately precise ideas of the prey actually available to an orb weaver in a given habitat.

Calibration studies which compare trap captures with the captures of orb weavers in the same habitat are unfortunately uncommon, but also suggest the need for skepticism about the usefulness of sticky traps. The most complete study (Castillo and Eberhard 1983) found a surprisingly poor the correlation between trap captures and spider captures (in terms of numbers of individuals of different species). Trap catches explained only 23% of the mean squared variation in prey in webs, despite large samples of insects (654 and 238 prey captured in traps in spider webs) the unusual care in mimicking the webs (traps were hung at exactly the same heights in the same fence at the same time of night and at the same angle with the wind as the spiders’ webs).

Still another complication is that not all prey are equally nutritious (section 3.2.5.3). Many published data on prey have the serious disadvantage of being based on the numbers of prey, rather than their weights. Nutritionally, larger prey will tend to be more valuable than smaller prey; Perhaps many or even most of the species of prey in they typically long lists of prey species (section 3.2.5) are nutritionally irrelevant. Take, for instance, the possibility that one species’ orb was designed to capture dragonflies and damselflies (say it is designed to have reduced visibility, and to increase interception rather than retention, because odonates are probably easily retained by their large wings and abdomens), and that a second species’ orb was designed to capture large beetles (e.g., designed to resist high-energy impacts, with traits like dense sticky spirals and a vertical elongation to combat tumbling escapes). Webs with both designs could also capture a long list of small flies, aphids, small leaf hoppers, etc., and thus be classified as generalist orbs, even though these other prey were in some sense incidental by-products. Or take an inverse case, such as that of *Tetragnatha montana* (TET), in which counts of prey indicate that Diptera, and especially mosquitoes (Culicidae), are the main prey (40%) (Łuczak 1970; Riechert and Łuczak 1982). Even if the percentage of mosquitoes were doubled, their nutritional value might still be unimportant nutritionally compared with other, larger prey (Blackledge 2011). Evaluations of relative nutritional importance are even more difficult when study sites often do not resemble those in which the spiders evolved (e.g., the anthropogenic habitats where many studies have been performed) (see below).

Now add to this the recent findings (summarized by Toft 2013) that for generalist spiders, many prey (“possibly the majority”) are of low nutritional quality (quality was defined as the potential contribution to the fitness of the spider). The nutritional benefits ranged from complete to null to detrimental, even within a single taxon such as Collembola or Diptera. Low quality was primarily due to defensive toxins, and to a lesser extent by the presence and absence of particular nutrients. Worse still for the hope that one can accurately quantify nutrition from prey counts in the field, the quality of some prey varied depending on the other prey that the spider captured. For instance, aphids, which were consistently of very low quality in monotypic diets, enhanced fitness at least somewhat when they were part of mixed diets. In sum, these problems shake my confidence that published studies of the prey of web spiders in which no corrections were made for nutritional value (the overwhelming majority) can provide reliable benchmarks for modeling studies. The numbers, sizes, and qualities of different prey are important, and require additional data that are generally not available.

Major variations in the prey captured by a given web type are not, by the way, limited to orb weavers, and can involve some surprises. A giant sample of >3000 prey from the substrate webs of the filistatid *Pritha* (= ?*Filistata*) *nana* on a wall in Camerun, the most common prey (by numbers) were nematocerous flies (31.0%) (Nentwig 1982), a group that generally flies rather than walks; ants and woodlice were nearly absent (1.6%). In contrast, another filistatid with a similar substrate web, *Filistata insidiatrix*, mostly captured walking prey (83.3%), with ants and woodlice comprising 66.7% of the total (Nørgaard 1951). In the scytodid *Scytodes longipes*, an anthropic spitting spider which builds a small tangle of non-sticky lines that apparently serves mostly to orient the spider's attacks rather than as a trap, more than half of the prey captured indoors in houses in Panama were in a single family of flies (Psychodidae); this family was so rare, however, in the prey captured by the same spider species on the outer walls of the same houses that it was not even listed separately (psychodids were presumably among the 7.3% of "other Nematocera") (Nentwig 1985*a*). Similar surprises sometimes also occur in orb weavers; for instance, 5 of 7 prey in the webs of *Meta menardi* (TET) were strictly pedestrian (millipedes) (Yoshida and Shinkai 1993).

Summing up these various sources of uncertainty regarding attempts to measure the prey actually available to orb weavers, there is reason to have serious doubts regarding their accuracy. It is very difficult to translate counts of prey collected in an environment of a web into measurements of the nutrition that is truly "available" to a given spider in that environment.

O3.2.4 Variation IV: "The" habitat

The prey captured by some species varied substantially from one habitat to another (e.g., Bilsing 1920; Robinson and Robinson 1970*b*, 1973*a*; Riechert and Łuczak 1982; Shelly 1983, 1984; Nyffeler and Benz 1978*a*, 1978*b*; LeSar and Unzicker 1978; Nentwig 1985*b*; Ludy 2007; Blackledge 2011). Take, for example, ten studies of species in the relatively well-studied genus *Argiope* in which different species appear to have relatively similar orbs (e.g., Wiehle 1928; Kaston 1948; Witt et al. 1968; Reed et al. 1969, 1970). The percentage of Diptera (in terms of the numbers) ranged from 1.3% up to 80% of the total catch, and the frequencies of other groups also varied substantially: Coleoptera from 0.5% to 22%; Lepidoptera from 0.3% to 36%; and Odonata 0 to 32% (summary in Eberhard 1990*b*). Within a single species, *A. aurantia*, the portion of odonates in the prey varied from 0 to 32% in only three studies. The lesson is that surveying the prey captured by a species with a given orb design in one or only a few habitats may not be enough to obtain a reliable benchmark for modeling studies.

One illustration of the difficulties of possible habitat variation comes from work on the sympatric araneids *Neoscona punctigara* and *N. mellotteei*, which build more or less typical orbs. These species differed in the fraction of their total catch were beetles (elaterids, weevils, and carabids) (Yamanoi and Miyashita 2005). They were said to inhabit the same microhabitat, as measured as percent plant cover and web height, but the samples were small, and the percent plant cover is only one of several aspects of a habitat (e.g., species of plants, living vs. dead plants, the sizes of the open spaces in which webs were built) that might be important. The possibility remained that, even here, prey differences between these species were due to differences in web sites rather than to differences in web designs. Similar possible differences in subhabitats among five species in a seasonal rainforest habitat (Craig 1987*a*) lead to similar doubts regarding conclusions relating orb design to prey captures. Both Riechert and Łuczak (1982) and Wise and Barata (1983) concluded from their own data and reviews of other studies that differences between microhabitats influence prey captures more than differences in web structure.

Without such controlled experiments (for instance, experimentally placing different types of orbs at chosen sites in nature), I do not find it easy to know which possible differences in web site traits may or may not have important consequences on prey. I must note, however, that some studies suggest that perhaps these worries may be overly cautious. Riechert and Cady (1983), working with species that build both orbs and non-orbs in an apparently relatively simple biotic environment (spaces under ledges in sandstone cliffs on heavily vegetated slopes in the Appalachian Mountains), found that four species with very different web designs captured surprisingly similar arrays of prey: the theridiid *Parasteatoda* (= *Achaearanea*) *tepidariorum* built a tangle with gumfoot lines; the araneid *Araneus cavaticus* built orb webs; the agelenid *Coelotes montanus* built substrate sheet webs; and the hypochilid *Hypochilus thorelli* built a largely aerial sticky sheet attached broadly to the substrate. The details of where the webs of these species were sited on the ledges were not identical, yet their prey were very similar. Discriminant analyses showed nearly total dietary overlap for *Araneus*, *Coelotes* and *Hypochilus* (Fig. 3.3, Riechert and Cady 1983) (prey were identified only to order, however, and it was not clear whether prey numbers were adjusted for prey weights).

One additional, "ecological realism" problem concerns the degree to which the habitat in which spiders and their prey are studied resembles the habitats in which the spiders evolved (section 3.3.4.2.2.2). A species' survival in a recently altered habitat demonstrates that it is able to survive the conditions there, but not that its traits represent specializations to adjust to those conditions. The fact that a species survives and reproduces in a corn field, for instance, is an incidental consequence of its adaptations to other, natural habitats.

O3.2.5 Temporal variation

The changes in prey from one season of the year to another can be striking. The temporal variance in prey capture was so large that *Tetragnatha elongata* (TET) may be unable to reliably distinguish good web sites from bad (Gillespie and Caraco 1987). Quantified by the biologically important measure of weight, about 55% of the prey of *A. argentata* in an especially extensive study Panama were in only two orthopteran families, Acrididae and Tettigoniidae, but 62% of the total prey and 17% of the estimated total biomass were stingless bees in the genus *Trigona*. These bees showed striking temporal variation; during some periods in the dry season (when canopy trees were in flower) they were entirely absent (Robinson and Robinson 1970*b*). *Nephila pilipes* (NE) also showed strong seasonal variations between dry and wet months (Robinson and Robinson 1973*a*). Studies of prey availability generally include only one site and one season (Higgins' work on *Nephila* is an exception, with three sites and two seasons, but even this admirable effort yielded only a small sample, especially considering the wide geographic and habitat range of this species).

In sum, it is much more difficult than might be supposed to obtain reliable estimates of the sizes and identities of the prey that particular species of orb weaving spiders evolved to capture. The apparent advantage of orb weavers in determing the payoffs from variations in foraging behavior turns out not to be as strong as supposed. Ecology is a difficult science (Rickleffs 2008).

O3.2.6 Ontogenetic changes (and lack of them)

A further, more obvious source of problems in understanding the functional significance of different orb designs, but one that has nevertheless apparently gone unremarked, is ontogeny. Although details of orb designs sometimes change as a spider matures (section 10.2), the orbs of immatures are usually more or less similar to those of adults. Nevertheless, while the designs of the orbs are similar, the properties of the lines with which they are made are strikingly different. The lines of immatures are much thinner and weaker (Eberhard 1986*a*, Craig 1987*b*, 2003). This means that orbs with more or less the same design operate under vastly different mechanical circumstances, and on very different arrays of potential prey. To be able to evaluate statements about optimality, it would seem necessary to perform the extraordinarily difficult task of evaluating the effects of a given design feature over the entire lifetime of the spider. Arachnologists in general have tended to focus on the adult stage, but I see no theoretical justification of this "adultophilia" (section 3.2.14). It could even turn out that some design traits evolved to optimize the orb's functionality at a given key ontogenetic stage, and that its occurrence at other stages is an incidental, selectively unimportant consequence. The ideal would be to weight the advantages and disadvantages of each web trait over the different life stages, taking into account the constraints (if any) that a given design at one stage may impose on the designs at other stages, but current knowledge is far from this level of analysis.

Turning these thoughts about ontongeny on their heads, it may be possible to take advantage of ontogenetic changes by checking for correlations between these changes and other, ecological changes that also occur during the animal's development (e.g. spectra of prey sizes). This technique would have the advantage of at least largely controlling for phylogenetic innertia in the comparisons. Even here, there is the possible problema that the ontogenetic changes in orb designs show a trend for the designs of younger individuals to be ancestral when compared with those of adults (Table 10.1, section 10.2). One is left asking why, if leaving an open sector for the signal line in the web confers an adaptive advantage to adults of *Zygiella x-notata* (AR), immatures would fail to utilize the same trait?

One promising way out of this bind was taken by Barrantes et al. (in prep.), who compared the ontogenic changes in orb design of closely related species of the genus *Leucauge* (TET). The logic is that if the ontogenetic changes in two species differ, they cannot be due to the younger forms resembling the same ancestor. They found that in *L. argyra* the orbs of young nymphs differed from those of adult females in having larger numbers of radii and sticky spiral loops; in *L. mariana*, in contrast, there was essentially no ontogenetic change in either web trait. In both species, the distances between sticky spiral loops increased gradually as the spiders grew larger.

In summary, ontogenetic changes in orb design are often relatively small despite huge ontogenetic changes in the sizes and identities of the prey of the spiders, and of the biomechanical properties of their silk. And attempts to analyze the ontogenetic changes that do occur in terms of selective advantages are bedevilled by the common pattern for web ontogeny to retrace phylogeny, seemingly without clear relation to functionality, but comparisons of ontogenetic changes in closely related species offer a possible solution.

O3.2.7. Other variables that vary widely

Large variations in other variables represent still further challenges for modeling attempts. These include the time needed by the prey to escape once it has been stopped (Strohmenger and Nentwig 1987, Zschokke et al. 2006) (section 3.3.3.1), the effects of satiation on attacks (Herberstein et al. 1998, 2000), and the effects of previous learning on the rapidity of attacks (new prey were avoided by *Linyphia*) (Turnbull 1960). The variance in escape times for sepsid flies in the webs of the tetragnathid *Leucauge mariana* was so large that there was no effect on escape time when comparing retention times in intact, unmodified orbs with those in tattered orbs in which sticky spiral spacing had been modified by the struggles of many previously trapped flies (Eberhard 1989; see also Blackledge and Eliason 2007 for experimental web alterations. Perhaps if the samples in these studies had been large enough, the alterered patterns of sticky silk would have resulted in differences in retention times, but the lack of effects from the striking web alterations is impressive. It is important to keep in mind that large sample sizes are biologically realistic, because selection on a given spider's building behavior will be on the basis of all the webs that she builds in her lifetime. Nevertheless, the randomness with respect to how most prey interact with a web (the site in the web of their impact, the angle of the impact, the portions of the prey's body that contact sticky lines, whether or not any body parts are snagged on lines) means that even though selection may act on particular design details such as the number of radii and the distances between loops of sticky spiral, its effects must be relatively weak with respect to different types of prey.

There is also potentially important variation in prey struggling behavior. Some prey "played dead" for up to several minutes after being stopped by a web (section 4.11). This separates the prey impact stimulus from the vibrations produced as it struggles to free itself, and may reduce the chances the spider will attack, as the combination of these stimuli was especially effective in eliciting attacks by *Zygiella x-notata* (AR) (Liesenfeld 1956). Large variances of these sorts will result in weakening of selection in favor of any particular orb design, and thus in the biological relevance of general arguments derived from models and simulations (e.g., Eberhard 1986*a*).

Variation may also be important in a very different context – that of year-to-year changes in general prey abundance. For instance, the "rare large prey" hypothesis emphasizes rare events that have a high intrinsic variance, and the overall payoffs to spiders in terms of weight gain (growth, egg production) from prey capture. An alternative possibility is that the major determinant of evolutionary success was survival in periods of prey scarcity (say a lean season, or a crisis year every 5-10 years), in which case it could have been advantageous for spiders to reduce their variance in feeding success and thus the chances they would die of starvation. Increased specialization on the more consistent payoffs from smaller prey, which are more abundant and give more reliable payoffs, might be favorable in especially lean years, for instance, even if the mean total food intake summed over good and bad years were smaller (Blackledge 2011). I do not know of data that can resolve the question regarding relative importance of different tatics for any particular species. The possibility that smaller spiders are more likely to suffer from negative energy balances due to their relatively large nervous systems (Eberhard and Wcislo 2011) suggests that starvation may be especially important in the earlier ontogenetic stages of many species.

O3.2.8 Tradeoffs between functions

There are several types of tradeoffs in orb designs (Table 3.1), and it can be difficult to quantify them: there are a large number of possible web functions, and many have contradictory effects on different web functions; there are large variations in the effects of web design on several key variables (and thus the practical difficult of quantifying their effects precisely); it is often difficult to determine the magnitudes of the effects under evolutionarily realistic conditions (e.g., habitats similar to those where the spiders evolved); and there is no readily quantifiable common currency for measuring different costs and benefits (next section).

One of the most serious problems is quantifying contradictory effects. It is not sufficient to simply determine the direction ("polarity") of the effect of a given variable (e.g., increase vs. decrease prey retention times), as is often the case in behavioral ecology. Instead it is necessary to quantify multiple effects with enough precision to accurately *quantify* the balance between costs and benefits, and decide which is larger. This requires accurate answers to quantitative questions that are difficult to solve. For instance, *how much* does reducing the spaces between sticky spiral loops by say 0.1 mm increase retention? *How much* does an increase in retention time increase the probability of capture? *How much* does the trait simultaneously reduce prey interception? *How much* more material does it cost? The precision needed to answer these types of questions, especially under evolutionarily realistic conditions, is much greater than that which we behavioral ecologists are accustomed to providing.

O3.2.9 Different currencies

Combining the effects of differences in the many different web functions into a single measure of the effect on the fitness of the spider that made the web is, to say the least, a difficult task. Theoretically one could simply determine the effects of a web variables on the fitness of the spider (numbers of offspring contributed to the next generation). In practice this is seldom possible (even combining survivorship and fecundity in adult females is not adequate, because survivorship and growth as immature stages with similar orb designs is not included).

Converting the different web functions, measured in the capture of prey, in protection from predation, in energy expended, and in material expended, to overall fitness has not been attempted. Evans (2013) dealt with this problem by converting web payoffs to growth and survival, but had to make various weakly documented assumptions regarding frequencies of prey sizes, uniformity of nutritional values, and duration of retention in the web, and omit other variables such as the behavioral costs of finding appropriate sites and of building webs, web visibility, and web susceptibility to damage in order to do so.

Other studies have employed estimates or indicator variables, such the change in the amount of silk invested, changes in the amount of energy needed to build the web, changes in the total weight of prey captured. These tactics are reasonable for studies attempting to determine polarities. But balancing different costs and benefits against each other when they have only been estimated indirectly and measured in different units is difficult or impossible. How many future offspring would be represented by the cost of synthesizing one additional mg of silk to be spent in orbs to give them thicker lines? How many additional mg of food would such an investment in thicker lines be likely to yield, and how many more offspring would be produced as a result?

O3.2.10 Biological realism – further calibration of models

Good modeling studies often include empirical checks of estimates made by the model or parts of the model. The quality of these checks can affect the quality of the model. Thus Sensenig et al. (2011) checked their model of the maximum stopping potential of an orb (based on the combined breaking energies of all silk lines in the capture area per unit of area) by studying the energy absorption of the orbs of four species with high-speed video recordings of the impacts of objects, and found a tight correlation between the two. But crucial data to evaluate the quality of this check were not specified. In particular, neither the size nor the shapes of the object (flat sheets? spheres?) nor the site in the web where impacts occurred were specified (the closer to the hub the object strikes, the more radii it will contact and the greater the energy that can be absorbed), other than the note that the projectile "directly contacted at least one radial and five spiral threads". The sites of impacts were apparently not systematically varied to give proportional coverage to different portions of the orb which have different stopping abilities (section 4.3). The fact that radii nearer the edge of the orb are farther apart, are under more tension due to forces applied by the sticky spiral (Eberhard 1972; Zschokke 2000a), and, in some species at least, are composed of twice as many fibers (Zschokke 2000a,b), means that the site of impact could have a substantial effect on an orb's ability to stop prey. I believe that this paper is easily the best comparative study of the functional significance of different orb web designs ever attempted. Its large sample, wide taxonomic coverage, inclusion of data on different biomechanical properties of the silk lines, and careful use of phylogeny set high standards; no other study of orb design that has come close to matching it in these respects. But this weakness (as well as others mentioned in section 3.2.7.5 related to variability in prey properties that can affect stopping and retention) make it difficult to evaluate the reliability of its conclusions.

O3.3 Possible relations between silk composition, prey impact traits, and orb designs

Perhaps not surprisingly, the chemical composition and properties of lines vary according to what the spider has eaten recently (Madsen et al. 1999; Craig et al. 2000; Tso et al. 2007; Boutry and Blackledge 2008; Blamires et al. 2010*a*). At least some of this unexpected variation may be the result of adaptive manipulations by the spider, and the frequencies and magnitudes of adaptive vs. non-adaptive variation in silk characteristics are promising but as yet almost completely unexplored. One possible adjustment mechanism is opening or closing valves in silk gland ducts (Wilson 1962; Ortlepp and Gosline 2004; Blackledge 2012). A second, studied in *Nephila pilipes*, is selective expression of different spidroin silk genes (Blamires et al. 2010*a*). Still another possible source of variation in the properties of homologous lines is mechanical fatigue, which can result when lines are repeatedly stressed (section 8.5.5.4).

A more surprising possibility is that the structural properties of a spider's silk may be adjusted in accord with the kinetic energy of the prey on which she has recently fed. Stronger lines (radii with greater structural "stiffness) were produced by mature female *Nephila* *pilipes* (NE) after feeding on live higher-energy prey (about 300 mg crickets) than when they were fed with live low kinetic energy prey (approximately 60 mg flies) (Tso et al. 2007). The conclusion that the spiders altered the properties of their silk in anticipation of further high-energy impacts can only be tentative, however. On the one hand, it is highly likely that the nutrient profiles of the crickets and flies differ, and a separate experiment that isolated the effects of nutrients and prey vibrations did not give clear results. When dead flies were paired with fly vibrations, radii were less stiff; there were no differences, however between the other three combinations (dead crickets paired with fly vibrations, either dead flies or dead crickets paired with cricket vibrations (Blamires et al. 2011) ("stiffness" in this study was apparently a combination of elongation, tension, and effective length). In the wild this species captured a wide variety of prey, and it is unlikely that crickets form an important part of their diet (Robinson and Robinson 1976), so specific adjustments to this type of prey seem unlikely. There is also the question of the degree of stochasticity in prey captures on successive days (how much more likely is it that cricket will be captured tomorrow if one was captured today?). In sum, this cause-effect relation would be surprising if it occurs.

Another study (Boutry and Blackledge 2008) also found differences in silk properties in *Parasteatoda* (= *Achaearanea*) *tepidariorum* (THD) when they were fed either crickets or isopods (pill bugs), but noted that the changes in silk properties might have resulted from incidental correlations in chemical properties of the food, or from the effects of the greater weight of spiders that were fed crickets.

Differences in the chemical and physical properties of the silk may also be related to design differences in orbs. The most substantial step in this direction is the study of Sensenig et al. (2011), with data from 22 species. Unfortunately, their conclusion that evolutionary shifts to larger body sizes were repeatedly accompanied by improved web performance because of changes in both silk material and web design are difficult to evaluate. The first problem was that the "performance" of each web design was evaluated solely in terms of the web's ability to stop prey, ignoring all other possibly important functions (interception, retention, visibility, mechanical stability, etc.), some of which are reduced by traits that improve the stopping function (Table 3.1). Secondly, the analyses combined diverse variables into "principal component" variables. For instance, web design component #1 (called "quantity" in the discussion), had factor score coefficients of 0.76 for web area, -0.69 for radii count, 0.79 for radial diameter, 0.75 for spiral diameter, and 0.87 for the distance between sticky spiral loops; a "quality" component had factor score coefficients of 0.88 for radial strength, 0.45 for radial strain, 0.82 for radial toughness, 0.88 for sticky spiral strength, 0.38 for sticky spiral strain, and 0.84 for sticky spiral toughness. The biological significance of such complex mosaics of traits is not clear (and is surely mis-represented by such simple labels such as "quantity" and "quality").

O3.4. The function(s) of silk stabilimenta: critical evaluations of the evidence

The tables in this section present the data on which the discussion of the functions of silk stabilimenta ("stabilimenta" in what follows) was based. Table O3.3 summarizes the data which has been used to argue for different possible functions for silk stabilimenta; Table O3.4 gives critical evaluations of the logical implications of these data for the four most widely cited possible functions (the conclusions are mine, and do not necessarily agree with those of the authors whose studies provided the evidence) (in many cases the author did not even discuss all of the four hypotheses); and Table O3.5 presents a more thorough critical examinations a set of studies which were particularly important in documdnting whether or not prey are attracted to stabilimenta in the field. The strengths of the confirmations and rejections vary widely among different hypotheses and types of data, and I have attempted to code these strengths and weaknesses in the tables, giving my reasons for the coding and my disagreements with authors in the footnotes.

Deducing the consequences of a given type of data for a particular hypothesis was not always easy. I will illustrate this with a relatively simple case. The question of whether the timing of web construction is appropriate for the web to be operated during the day (built around dawn) or to be operated at night (built after dusk or the first part of the evening) does not seem to be related directly to the mechanical stabilization or web strengthening hypothesis, so it would seem that the data are irrelevant for this hypothesis and should be coded as "-" in Table O3.4). But the trend in these data toward daytime webs having stabilimenta is not predicted by the strengthening hypothesis but is predicted by other hypotheses, so they constitute evidence against web strengthening (hence the "A_4" in Table O3.4). In fact, the trend toward daytime webs is so strong (there is not a single species known that builds a stabilimentum on a nighttime orb) that the data represent very strong evidence against the mechanical stabilization hypothesis as a general explanation. In other cases, with weaker or less well-documented trends, or when the hypothesis could be modified *post hoc* in a more or less convincing way to accommodate the data, decisions of this sort were more difficult. I realize that my evaluations of the strengths of rejections and confirmations are not quantifiable, and are sure to be questioned by some. I can only say that they are my best attempts to provide guidance in this dense tangle of data.

BOX O3.1 Uloborid stabilimenta: multiple lines of indirect evidence point (mostly) to one conclusion

"The immobility of the spider, her position at the centre, her elongated posture, her accurate adaptation to the width of the gap [in the linear stabilimentum], her fixed attitude in line with the ribbon and the structure of the ribbon in harmony with herself, each has a place in the multiple combination developed for the production of a concealing effect." (pp. 210-211 in Hingston 1925 on the uloborids *Uloborus* sp. and *Zosis geniculata* (=*U. ceniculatus*).

Most of the many published observations on stabilimenta are hidden away in the tables O3.3-O3.5; this box is intended to give the reader a sample of the biological richness of the different kinds of evidence, and the conclusions they can suggest. Lubin (1986) summarized previously scattered knowledge regarding the stabilimenta of uloborids. She found that uloborid orb weavers are monotonously uninventive in several of the aspects that are mentioned in the quote from Hingston: they all build daytime orbs; they nearly all rest at the hub during the day; they usually assume constrained postures during the day that obscure the visual outlines of their legs; and they nearly all build silk stabilimenta. The typical constrained posture in the large genus *Uloborus*, with legs I and II extended anteriorly and pressed tightly together, causes the spider's four anterior legs to appear to be a single curved object broadly united to her body. Two morphological modifications that make this posture possible: an anterior narrowing of the cephalothorax; and a prolateral notch or bowing of the femur of leg I (Opell and Eberhard 1984). The spider's visual camouflage effect is heightened by both colors and setae. The tips of legs II are held against the thick tufts of setae on legs I, thus obscuring them (Opell and Eberhard 1984). And the distal portions of leg I have black and white bands, or dark tibial setal tufts combined with light metatarsae and tarsae that further obscure their outlines (Muma and Gertsch 1964; Opell and Eberhard 1984), thus making them appear to end at the tibial tuft. In those *Uloborus* species that build linear silk stabilimenta, the spider preferentially orients herself at the hub so that her extended front legs are aligned with, and thus blend visually with the stabilimentum, and her body just fills the space between the arms of the stabilimentum (Hingston 1927, 1932; Marson 1947*a*, 1947*b*; Eberhard 1973; Lubin 1986; Opell and Eberhard 1984). Several of these traits parallel those of visual crypsis in insects such as walking sticks (Robinson 1969).

Visual camouflage could function to reduce the danger of being spotted by visually orienting predators (the visual defense hypothesis; #4 in Table 3.7) or by prey (an extension of the prey attraction hypothesis; #2 in Table 3.7). The visual defense hypothesis is favored over the other by the additional observation that in two species of *Uloborus* as well as in the related *Zosis geniculata*, spiders sometimes add stabilimenta to resting webs, which cannot capture prey because they lack sticky lines (se #8 in Table O3.3). The spiders sit in constrained, camouflaged positions (Opell and Eberhard 1984; WE), aligned with these stabilimenta.

Three species that are exceptions to these rules for typical uloborids also fit the visual defense hypothesis. B. J. Marples (1955, 1962) observed that *Daramulunia* (= *Uloborus*) *gibbossa* in Samoa often does not rest at the hub, but instead at the edge of its daytime orb, which is built low in herbaceous growth in forests, and was also unusual in that spiders dropped to the ground readily when disturbed, where its dark brown color provided effective visual camouflage. As predicted by the visual defense hypothesis, this species was also exceptional in almost never building stabilimenta. This otherwise improbable combination is not predicted by the prey attraction hypothesis (in fact, this species might have been expected, if anything, to be in special need of prey attraction due to its presumably slower attack behavior, which must be launched from the edge rather than the hub of the orb. A second uloborid lacking stabilimenta is *Philoponella arizonica* (Smith 1997). In contrast with its congener, *P. oweni*, which lives in similar habitats and usually builds stabilimenta, *P. arizonica* makes more extensive tangles of lines above and below its orb (Smith 1997); it may thus be less exposed to predators. A third exception is *Uloborus eberhardi*. This species also builds a daytime orb, but its web is unusual in having a thin twig passing through the middle of the hub. The spider rests appressed to the underside of the twig, with her anterior legs extended forward and hidden from view (WE). As expected under the visual defense hypothesis, this species also lacks a stabilimentum.

The uloborid *Polenecia producta* also has a twig through the center of its modified orb web; the details of the placement of its tiny stabilimentum reinforce the visual defense idea (Fig. 3.44). Hans Peters (1995) showed that *P. producta* rests with her legs I hidden under the twig, where they are unable to monitor vibrations from her web. Instead, her shorter legs II are spread slightly, and hold hub lines close to the twig (Fig. 3.44b). The stabilimentum consists of only a small sparse array of white lines alongside the twig, just where tarsi of legs II grasp the hub lines (Fig. 3.44c). The stabilimentum of *P. producta* thus seems to function much like the tufts of setae on tibia I of *Uloborus*, to hide the tips of the spider's legs II, or the tufts on the femora of *Deinopis* sp. that hide their margins (Getty and Coyle 1996). It takes a stretch of the imagination to suppose that the highly reduced stabilimenta of *P. producta*, which are placed exactly where the spider puts the tips of her legs, function as a prey attractant rather than as visual camouflage.

Other orb-weaving uloborids have different combinations of similar traits. *Zosis geniculata* has a whitish grey body color that resembles that of the disc stabilimentum that she nearly always adds to the center of her hub (Fig. 3.46). The camouflage is especially effective, at least for human eyes, when the spider is seen from below in the dimly lit situations where they live (e.g., close to ceilings inside buildings or other protected sites). These spiders also often build linear stabilimenta, and rest with their long legs I held close together (Opell and Eberhard 1984) and directed anteriorly and aligned with the stabilimentum (WE) (Fig. 3.46). The sharp black and white bands on the front tibiae, and on tibia II and tibia, metatarsus and tarsus IV, break up the legs' visual outlines (Fig. 3.46).

Species in both *Uloborus* and *Philoponella* show another exceptional trait that emphasizes a further aspect of stabilimentum biology. In both *U. diversus* (Eberhard 1973) and *Philoponella herediae* (Opell 1987) the spider sometimes adds stabilimentum silk to non-sticky lines below the hub. These lines, which are sometimes lax and are in general not under enough tension to deform the radial and frame lines to which they are attached, could function as visual defense; they could distract predators searching visually for a spider hidden among white silk lines (Opell 1987), and induce it to focus its attention away from her immediate vicinity. Or they could deter a predator from approaching the web, by advertising the presence of a barrier (in accord with the web advertisement hypothesis). They would seem difficult for the prey attraction hypothesis to explain, because they would draw prey away from the immediate vicinity of the sticky lines of the orb (the orb described by Opell was 30 cm above the forest floor and at 35° with horizontal). Our current ignorance regarding the identity of prey and predators in the field, and their behavior in the vicinity of orbs renders further speculation on this point fruitless. The frequent absence of observations under ecologically realistic conditions is a serious impediment to resolving the "stabilimentum wars" (Table O3.4).

Just as with other groups of orb weavers, however, the data from uloborids do not uniformly support the visual defense hypothesis. Several species of *Philoponella* built modest-sized linear stabilimenta, but crouched at the hub, with legs I folded tightly against the ventral surface of the cephalothorax (Opell and Eberhard 1984). The spider's legs were near to but not contiguous with the stabilimentum, and neither the positions of the legs nor the spider's often dark coloring promoted her blending with the stabilimentum. The crouched positions and disruptive coloration of the legs of *Philoponella* spp. (Muma and Gertsch 1964; Opell 1979; Opell and Eberhard 1984) leave little doubt that these spiders have been under selection to defend themselves against visually orienting predators; but the role (if any) of their stabilimenta in promoting this defense is not clear. It is not certain whether the weight of this evidence against the visual camouflage hypothesis is enough to call into question the conclusion drawn from the several confirmations listed above.

Box O5.1 The domed sheet plus tangle web of the pholcid Modisimus guatuso

The relatively rapid web construction by the pholcid Modisimus guatuso (lasting as little as about 15 min), and the ease with which it could be elicited during the daytime at geometrically simple sites (indentations in tree trunks) by destroying nearly all of the previous web (except a small tangle of lines near the trunk) facilitated a preliminary description of its construction behavior (Eberhard 1992*b*). Happily, this species illustrates some patterns that seem to be common in other non-orb species.

The web of *M. guatuso* consisted of a dome-shaped sheet with a sparse tangle above and sometimes a few lines below (Fig. 5.2). Webs were often built in indentations in a large object such as of a large tree trunk. The dome of the sheet was asymmetrical, with its peak on the side of the sheet that was nearest to this object. Three types or modules of behavior occurred repeatedly during the construction of a given web: extending the skeleton web; filling in the skeleton web with a sheet; and filling in the sheet with sticky lines.

Web construction began when the spider extended the small tangle by moving back and forth along its most exposed side, using her dragline to make up to six successive extensions on alternate sides of the same edge of the web (Fig. 5.1a-c). Some lines laid in the early stages of extension were above the curved plane where the sheet would eventually be located, but later extensions tended to be lower and to form the plane of the sheet. Most extensions were added to the edge farthest from the trunk. In some webs but not others the spider dropped at least once 1-5 cm on her dragline in an apparently exploratory trip, then ascended without having made an attachment.

Bursts of filling in the skeleton web were intercalated between bouts of extending the skeleton web. The spider moved in the space encompassed by web lines, attaching her trail line to many of the lines she crossed. Each attachment was made by moving her abdomen ventrally (upward) toward the web line to which her dragline would was being attached (the “attachment line”). At least one leg III held the attachment line anterior to the attachment site at the moment of attachment; sometimes both legs III grasped this line just anterior to her spinnerets. More rarely the leg IV opposite to her leg III also held the attachment line just posterior to the attachment site. In one case, one leg II also held the attachment line just anterior to the leg III. This variation contrasted with the very rigid use of only ipsilateral legs III and IV by orbicularians (Fig. 6.12, section 6.5). It was not certain whether any legs consistently held the trail line just before or during attachments.

Most skeleton filling in occurred in the central area of the web, especially near where the top of the dome of the finished sheet would be. Filling in the skeleton web differed from skeleton web extension in that spider always never turned back just after making an attachment to walk along the line that she had just laid, even when the attachment was to the substrate. As during web extension, the spider consistently moved beneath lines already laid, very seldom climbing up past a line to make an attachment (two exceptions were seen). As a result, most lines laid while filling in the skeleton formed bridges under the more upward projecting portions of the web laid earlier. Usually successive lines soon came to be concentrated in the plane where the sheet would be.

Extending and increasing the density of the skeleton web lasted 3-10 min. In the “finished” skeleton web, the mesh was densest where the top of the dome would be, often forming a small, nearly horizontal platform of relatively uniform mesh that was approximately the size of the spider as she rested on the web (Fig. 5.2). This area had a tangle of lines above it, and was surrounded by a more or less planar extension that was progressively less densely meshed farther away from this central area.

The final step was to fill in the sheet, which generally took 5-10 min. She walked in approximately straight lines back and forth across the skeleton sheet, repeatedly drawing silk from her spinnerets with her legs IV. These legs pulled a line (or lines?) and pressed it ventrally (upward) against the sheet, where it adhered. The legs IV usually moved nearly synchronously upward, with one lagging slightly behind the other. Occasionally the legs moved with alternate upward strokes as in another *Modisimus* species (Eberhard and Briceño 1985). Only occasionally did the spider attach the line to the sheet with her spinnerets. These attachments were made almost exclusively at the edges of the sheet, and were immediately followed by the spider moving abruptly toward the center. This produced a “V” configuration (Fig. 5.2c). Favorable lighting revealed that lines that were presumably laid during “fill in” behavior were not tense; they sagged when loaded, and moved slightly in weak air currents (Fig. 5.21).

Few, relatively simple organizing principles appeared to determine the order in which lines were added during the construction of a *M. guatuso* web. The spider extende the area of the web in stepwise increments by moving back and forth along one more exposed edge and, when she encountered the substrate, moving farther along the substrate away from the web center; then she attached this trail line to previously laid lines as she returned to the central area (Fig. 5.1a-c). Subsequently she filled in the space between the new sides by “wandering” across the sheet with two additional sets of lines, the non-sticky and perhaps stronger lines that were attached frequently to the skeleton lines with piriform attachment discs and laid under tension, and the sticky lines that were laid with few direct attachments to the other lines and were not under tension.

This “extend the edges and then fill in” pattern occurred in both the horizontal and vertical dimensions, but was most accentuated horizontally. The planar nature of the sheet resulted in part from the successive attachments to the substrate that extended the web being made in more or less a single plane. Presumably the same organization of construction behavior occurred in other pholcids that had similar sparse domed-sheet designs, such as *Mesabolivar* sp. (#1384) (Fig. 9.15), though the lack of recognizable skeleton lines and the greater tangle above the sheet leave doubts.

O6.1. Further details of the behavior of A. diadematus and M. duodecimspinosa

This appendix complements section 6.3 of the text by mentioning further details and giving more extensive descriptions. To facilitate its use in this way, I have used the same sub-section titles in both.

O6.1.1 Stages of construction

Although experimental manipulations have shown that there is a certain amount of flexibility in the ordering of building stages (Fig. 6.2, sections 6.3.1, 7.10), it is clear that the stages are biologically "real" and not just human inventions. Throughout orb weavers, radius, hub and frame construction always precede temporary spiral construction, temporary spiral construction (except in species in which it is omitted) always precedes sticky spiral construction, and sticky spiral construction always precedes hub modification. In *M. duodecimspinosa* and *A. diadematus* the only major variations during normal, unmanipulated orb construction are minor: whether all of the radii are built before the first hub loops are begun.

Under expermental conditions, *M. duodecimspinosa* demonstrated a previously unappreciated flexibility to interrupt sticky spiral construction temporarily to lay additional non-sticky lines (Fig. 6.2): a mature female responded to having ten radii cut experimentally during sticky spiral construction by interrupting the sticky spiral briefly and making a modest repair with non-sticky lines in the broken sector. The repairs were not particularly effective in improving the uniformity of the spacing of the subsequent loops of sticky spiral in the damaged sector, because the spiders consistently added the non-sticky lines to the hole on the far side rather than the near (hub) side, where subsequent sticky lines were built (Fig. 6.2). This flexibility was inconsistent, however, as in some experiments the spider made no repairs and simply continued building the sticky spiral across the gap (WE). This responses contrast with reports by both Fabre (1917) and Hingston (1920) that similar experiments failed to elicit responses in either *Argiope bruennichii* (AR) or *Neoscona nautica* (AR); neither author mentioned how many times they repeated their experiments, so it is not clear whether these species may also be flexible.

O6.1.1.1 Exploration and establishing early lines

O6.1.1.1.1 Use previous lines or start from scratch?

M. duodecimspinosa resembled several other araneids, such as *M. horrida* and *M. sexspinosa*, *Acacesia hamata* (Carico 1986), and *Gasteracantha cancriformis* (WE), in removing most or all of its orb daily, and then beginning the next web from scratch. Careful inspection of the sites in the field where *M. duodecimspinosa* rested at night between orbs often revealed one or a few long lines; these lines occurred whether the spider had built an orb near this site the day before, or I had placed her there the previous evening. Few if any of these lines ended up being included in the next orb that the spider built. Nevertheless, their placement may have involved exploration. Sometimes construction behavior in the morning began after only a few trips along such lines to make small shifts in their attachment sites. Thus, at least preliminary exploration may occur hours before orb construction. It is unclear why species like *M. duodecimspinosa* and *G. cancriformis* so often removed all frame lines and submitted themselves to the vagarities of starting from scratch (section 6.3.2.2).

In many species, such as the tetragnathid *Leucauge mariana*, and the araneids *Neoscona* spp. (Hingston 1920; Carico 1986), *Argiope* spp. (Carico 1986), *Caerostris darwini* (Gregorič et al. 2011a), *Metepeira labyrinthea* (Carico 1986), *Cyclosa* spp. and *Allocyclosa bifurca* (Carico 1986, WE, Fig. 6.21), the spider replaced the radii and sticky lines in a previous orb with a few radii, leaving all or most of the frame and anchor lines intact, and then later reused these lines in her next orb. In a few, nephilid (*Nephila, Clitaetra, Nephilengys,* and *Herrenia*) (Kuntner et al. 2008a) and uloborid genera *Uloborus, Octonoba, Zosis* and *Philoponella* (Eberhard 1972, WE, Lubin 1986), spiders were even more conservative, often removing and replacing only a sector of the previous orb each day (see section 6.3.9).

The observations of *M. duodecimspinosa* floating lines to find attachment sites in nature has not been repeated in *A. diadematus*, whose building behavior, as far as I know, has only been observed in captivity. As Comstock (1967) noted long ago, however, floating lines must be common, as orbs are often built between trees or bushes above herbage which would have made it impossible for the spider to carry a line over the intervening ground. The many published drawings of spiders finding attachment sites by simply walking along the inner walls of a cage give serious misimpressions. Incidentally, observations of occasional failures by *M. duodecimspinosa* to find nearby attachment sites that were only 20-30 cm away and in plain view (WE) confirmed the idea that exploration to find sites is not guided by long-distance cues (section 8.4).

O6.1.1.1.2 Gathering sensory information

Although there is to date no supporting experimental evidence, I believe (as argued by Vollrath 1992) that it is likely that orb weavers utilize path integration information during exploration when they select the spaces in which they build their orbs. Judging by the sites where spiders end up building their webs, and by their responses to experimental modifications of the contours of the spaces that are available to them (Fig. 7.42, section 7.8.2, Tilquin 1942; Le Guelte 1966; Ades 1986, 1991; Vollrath 1992; Rao and Poyyamili 2001; Hesselberg 2013; Barrantes and Eberhard 2012; Eberhard and Barrantes 2015), exploration probably provides an assessment of the sizes and locations of the open spaces between the attachment sites in which the orb will be built. .

One common behavior during exploration in *M. duodecimspinosa* was removing lines already laid, and shifting their points of attachment, usually by employing "break and reel" behavior (Fig. 6.3, 6.4, Appendix O6.2). This behavior is crucial for the web to have an orderly array of lines, despite the preliminary lines attachments made during exploration that are needed because of the spider's inability to evaluate the dimensions of a construction site before actually moving around in it. I suspect that break and reel behavior is "difficult", in terms of the coordination between the legs, the palps and mouthparts (to break lines) and the spinnerets. It may be taxonomically limited to Orbicularia (Eberhard et al. 2008*a*), but no proper survey has never to my knowledge been done. Perhaps some movements, such as packing up loose silk with legs III and the palps after receiving it from legs I and II, were derived from movements that spiders use to climb up drag lines (Eberhard 1986*b*), but again I know of no analyses of appropriate data.

O6.1.1.1.3 The end of exploration and the hub transition

The first reliable sign in *M. duodecimspinosa* that orb construction was beginning was a long reattachment of an upper anchor line to the substrate (at 2 in Fig. 6.5b); this marked the beginning of construction of the first frame (in some cases there was a slightly earlier sign, when the spider strengthened the lowermost attachment to the substrate). Usually the radius built as part of this first frame line was attached near the end of the frame line (e.g. at 3 in Fig. 6.5), but in some cases the first radius to the upper primary frame was attached nearer the middle (e.g. radius 0_z in Fig. 6.10), and subsequent radii were built on either side of it.

The "hub transition" has been termed the transition from building the proto-hub to the hub (Zschokke 1996). At this stage the attachment points to the substrate were all established in *M. duodecimspinosa* (and apparently at least most were also in place in *A. diadematus*); the site of the orb and the area that it would occupy had thus been determined. The tension on the first frame line was raised by cinching it up as part of the hub transition in both species (note the loop of line reeled in and attached at 5 in Fig. 6.5d), just before the spider moved down the radius and lowered the hub (Fig. 6.5d). From this moment forward, the construction of susequent lines became more stereotyped.

The hub transition is not easily noted, and was first documented clearly by Zschokke in *A. diadematus*, using the video technique that he pioneered (Zschokke and Vollrath 1995a; Zschokke 1996). After learning what to look for from Zschokke's work, I have observed it consistently in *Micrathena duodecimspinosa* (and also *M.* sp. nr. *lucasi*). Zschokke and Vollrath (1995b) reported it in the araneid genera *Larinioides*, *Cyclosa*, *Zilla*, and *Argiope*, and I suspect that similar behavior occurs in many other orb weavers and was missed by previous observers. In uloborids the process of establishing the definitive hub was somewhat different, however (section O6.3.2.3).

As soon as *M. duodecimspinosa* had repositioned the hub, her radially directed walking movements during radius and frame construction became jerky. One possible explanation for this puzzling behavior (which has not been described in other species) is that it increases the speed at which silk is drawn from her spinnerets, and thus increased the strength of the line (section 3.2.9); but this is only speculation. The uloborid *Hyptiotes paradoxus* made apparently similar jerky movements during frame construction; Zschokke and Vollrath (1995b) speculated that they function as defense against visually orienting predators.

O6.1.1.2 The other "primary" frames

When building the second and third primary frames, *M. duodecimspinosa* less often "cinched up" the tension on the frame line (see Fig. 6.5). Nevertheless the frame tension subsequently decreased as the spider broke and reeled up each new radius as she returned to the hub (Fig. 6.5g). Sometimes the spider attached one end of the second or third frame line to the substrate rather than to the first frame (see caption for Fig. 6.5). All of 14 such double anchors in 28 finished orbs photographed in the field were at the upper rather than the lower end of a lateral frame line (WE; $Chi^2 = 14$, $df = 1$, $p < 0.001$).

The first radii to the second and third primary frame lines of *M. duodecimspinosa* were attached at or near the upper end of the frame (e.g., radii 0_w and 0_y in Fig. 6.10), and all subsequent radii to that frame were added below it. In some cases there were two radii rather than one radius to the same primary frame line (e.g., radii 0_x, 0_y in Fig. 6.10).

In *A. diadematus*, some details of primary (and secondary) frame construction are not yet clear. Coddington (1986*c*) stated that a new radius is built each time a new frame line is constructed, but Zschokke (1996) found that 19 of 47 frames were not accompanied by a new radius. There are many other variations in frame construction (e.g. types A, C, D, E in other species such as *Leucauge mariana, Nephila clavipes*, and *Philoponella vicina* – see Appendix 4.3), and I expect that *A. diadematus* resembles these other species in performing several different types of frame construction (as is indeed suggested by the 19 of 47 observations mentioned by Zschokke). In addition, Zschokke's verbal description (1996) includes only a single sequence of behavior and lacks mention of the attachment made to the newly laid frame line (at *z* in Fig. 6.5). An attachment at *z* apparently occurred in the construction of the first frame line in *A. diadematus* (see Fig. 2F in Zschokke 1996). Some literature descriptions of frame construction in *A. diadematus* appear to represent still further variations (e.g., Reed 1969). Probably *M. duodecimspinosa* is atypical in being so consistent.

O6.1.1.3 Secondary radii

Each time the spider returned to the hub from laying a new radius during most of secondary radius construction (section 6.3.3.2), legs I grasped lines on the far side of the hub while she was attaching the new radius. Usually, except in the later stages of radius construction (Fig. 6.7), she only turned somewhat following the attachment, and waved her leg oII in the next open sector in which she would lay a radius, and grasped the leading edge radius. Often leg oI grasped one or two radii ahead (depending on how many radii were already in place), but it then waved and grasped the radius adjacent to the leading edge radius; in some cases, leg oIII also waved repeatedly in the open sector. The leg oIV then moved forward, and both oIII and oIV grasped the leading edge radius (possibly on either side of oII). Leg oII then advanced to the radius held by oI, and a normal sequence of following began as the spider began moving outward along the exit radius to lay the next radius.

Construction of hub loops often began before radius construction was finished (section 6.3.3.4); the late radii were often preceded by especially clear exploratory movements of legs I and II. For example, just before building one radius which was the third radius laid after hub loop construction had begun (at about 6:00 in the orb), oI waved twice in the open sector where the radius would be laid (after oII grasped trailing radius that leg oI had been holding), and then grasped leading r. Leg oII then pawed once in hole, and grasped the leading radius that was held by oI. Then each pawed once more in hole and returned to grasp the leading radius. Leg iI then also seized the leading radius, and, following additional slapping, oII held the trailing radius and oI slapped in the hole while iI held leading radius. Finally both legs

I slapped in hole, iI grasped the leading radius again, and oI slapped in hole and then grasped the trailing radius while iI slapped in the hole at least twice more. Finally the spider left the hub, walking along the trailing radius.

The spider altered the tension on each new radius (as do many other araneid and tetragnathid species – Eberhard 1981*a*) when she broke the provisional radius and reeled it up while she was returning to the hub (Fig. 6.8a). The tension changes were evidenced by changes in the amount that the radius displaced the frame line (compare angles α_1, α_2, and α_3 in Fig. 6.8a). The tension decreased perceptibly the moment the spider attached her new drag line to its broken end just after breaking it, and often decreased further as the spider moved toward the hub. To my knowledge no mention has been made of these tension changes in *A. diadematus*, but their widespread occurrence in other species (in each of the 13 araneid and tetragnathid genera observed in Eberhard 1981*a*) suggest that they also occur in this species. There may systematic variation in these tension adjustments, as in *Zygiella x-notata* (AR) the tensions were higher on those radii that made larger angles with adjoining radii in finished orbs (Le Guelte 1969).

There may have been variation in the site along the radius where the spider broke it and began cut and reel behavior as she returned to the hub, but I have not observed this detail in *M. duodecimspinosa*. The araneid *Zilla diodia* tended to break the radial line nearer the hub (Zschokke 2000b) than did other araneids such as *A. diadematus* and *Larinioides patagiatus* (Zschokke and Vollrath 1995b), and *Z. diodia* also tended to break radii in the upper half of her orb closer to the hub than those in the lower half (Zschokke 2000b). Breaking the line nearer the hub would result in a longer portion of the radius being doubled; this would seem to be advantageous because it would make a larger portion of the radius better able to stop high energy prey without breaking. In this light, however, it is not clear why spiders break radii at any site other than very close to the hub.

O6.1.1.3.1 Radii at final angles

The "final angles" technique used by orb weavers (section 6.3.3) can be illustrated with radius 4 in Fig. 6.10. When this radius was built, there was an open sector between radius 2 and radius 0_x. Radius 4 was not laid at some intermediate point between these two radii, but instead near the exit radius (radius 2) at an angle that was not be subsequently bisected by any further radii (and was thus "final"). Exceptions to the "final angle" rule occurred occasionally (e.g. radius 44 in Fig. 6.10 was laid at an angle with radius 36 that was later subdivided by radius 58), but they were rare (see also Fig. 6.11 of *Uloborus diversus* (UL)).

One possible advantage of the "final angle" technique of radius construction is that it gives the spider more precise control over inter-radial angles than would some alternative patterns, such as bisecting each open angle with each new radius (as may occur, for instance, in the filistatid *Kukulcania hibernalis* – see Fig. 7.49). With the final angle technique, the spider can theoretically adjust each angle between the exit radius and the new radius to a precise value appropriate for the length of the new radius (see section 7.7.1.1). Only when she adds the final radius to an open sector does she leave an "uncontrolled" angle (the angle which is "left over" after the new radius is attached). In contrast, bisecting the sector technique offers much less precision.

O6.1.1.3.2 Upper exit radius

The tendency to use the upper of the two radii that were being grasped by legs I as an exit radius during radius construction is illustrated in Fig. 6.10. For instance, the exit radius when the spider built radius 4 in Fig. 6.10 was radius 2 rather than radius O_x; the exit used to build radius 50 (and the associated secondary frame) was radius 44, not radius O_y. This pattern was very consistent except when the two potential radii were both nearly vertical. In the web in Fig. 6.10, for instance, radius 39 rather than radius 37 was used as an exit when the spider laid radius 41; but radius 37 rather than radius 41 was the exit for laying radius 43.

One possible reason for using the upper of the two possible exit radii is that when the new radius under the spider's weight and the reduced tension when she breaks and reels she returns to the hub, she moved away from rather than toward the exit radius, reducing the chances of possible contact and mistaken attachments. It is clear that laying the new radius below rather than above the exit radius is not a mechanical necessity, because exceptions occasionally occurred (radius 11 in Fig. 6.10 was above rather than below its exit radius O_z; see also Zschokke andVollrath 1995a on *A. diadematus*).

It is interesting that the potential difficulty of sagging into previous radii while returning to the hub seldom or never caused problems. During the later stages of secondary radius construction in a vertical or nearly vertical web, the spider sagged downward during cut and reel behavior for more or less horizontal radii, bringing her body toward radii already present. For instance, while returning to the hub during the construction of radius 54 in Fig. 6.10, the spider's body sagged downward and was below radii 0_y, 3, and 5. In no case, however, has a spider of any species been seen to "mistakenly" grab such radii as she returned to the hub (it might, however, be difficult to observe such a mistake, especially if only legs I and II grasped intact radii). It would seem that the more nearly vertical the orb, the greater the danger of this type of a mistake. Perhaps species with truly vertical orbs make smaller or more careful movements of legs I and II during radius construction which minimize the lateral movements used to find and grasp the line (section 2.4.2), allowing the spider to consistently grasp the new radius rather than other nearby radii. There are no observations to test this speculation.

O6.1.1.3.3 Successive radii to opposite sides

The likely advantage of tending to lay successive radii on opposite sides of the orb is that it balances the tensions on the radii, and keeps the position of the hub more or less constant. In some cases, especially early in the radius construction stage, the spider seemed to simply move past the hub and out the other side to lay the next radius with no preliminary behavior that seemed to represent measuring angles. In contrast, exploratory movements of legs I and II in open sectors were especially distinct just before a new radius was laid later in radius construction. This interval between later radii has also been hypothesized to function to allow formation of additional silk in the ducts of the ampullate glands (Rawlings and Witt 1973).

O6.1.1.3.4 Hub loops

The leg movements of *M. duodecimspinosa* during hub loop construction were precisely coordinated and highly stereotyped Fig. O6.4), and closely resembled those previously described in *Leucauge mariana* (TET) (Fig. 6.12, Eberhard 1987*a*). The most striking pattern was that legs oI, oII, oIII and oIV all followed each other very rapidly and strictly in both space and time: each leg moved forward directly, with minimal exploratory waving, to the radius that was being held by the ipsilateral leg immediately anterior, and consistently grasped it either just inside (oII with relation to oI, oIII with relation to oII) or just outside (oIV with relation to oIII) of the site being held by the more anterior leg (Fig. O6.4c). During construction of the first loop or so of the hub, leg iIII was nearly immobile and remained in contact with a central point where the radii converged (Fig. 6.12a) (also seen in *L. mariana*). In contrast with *L. mariana* (Eberhard 1987*a)*, leg iIII released this hold during construction of the second or third hub loop (the later hub loops of *M. duodecispinosa* were much farther from the center of the hub than the length of leg III) (e.g., Fig. 6.12c).

I know of no record of "false starts" of radii during hub construction in *M. duodecimspinosa* or *A. diadematus*, such as those occasionally observed in the tetragnathids *L. mariana* and *Tetragnatha* sp., and *Gasteracantha cancriformis* (AR) (Eberhard 1981*a*). These other spiders sometimes interrupted hub construction to face outward briefly, and then moved away from the hub as if to lay a radius but stopped short, broke the exit radius and returned, replacing its inner portion. In less elaborate false starts the spider paused, turned to face outward briefly, holding adjacent radii with her legs I, but then returned to building hub loops. The less elaborate false starts may represent "mistakes" by the spider, in which she decided to lay a new radius (perhaps on the basis of information from legs oI and oII as she built the hub) but then changed her mind (perhaps on the basis of information from legs I as they held the two potential exit radii). The more elaborate false starts could also result from mistakes, or may function to adjust tensions on the radii (or both).

There were no extensive exploratory tapping movements by any of the outer legs or any other apparent attempt to contact the outer loop of the hub spiral. This raises the question of how the spider attached new hub loops with such constant spacing if she lacked precise information on the position of the previous loop. The probable explanation comes from video recordings of *M. duodecimspinosa* and the large, slow-moving species, *Nephila clavipes* (NE). Both performed a similar, small and quick movement of leg oIII just before each attachment. After having followed oII and grasped r_n, leg oIII slid inward along the radius a short distance until it encountered the outer loop of hub spiral (Fig. O6.4). This movement occurred just after leg oIV had moved forward to also grasp r_n, while the spider was bringing her spinnerets and r_n toward each other to attach the hub spiral to the radius (between the points grasped by oIII and oIV).

One further detail of hub loop construction by *Micrathena* spp., and perhaps in some other species, was that adjacent radii were occasionally attached directly to each other by a hub or temporary spiral attachments, producing a "false branching" pattern in which adjacent radii seemed to branch from each other (arrows in Fig. 6.10). The "branching" pattern was superficially similar to that seen in the hubs of *Uloborus diversus* (Fig. 6.11), where direct observations of behavior showed that it was generally due adding radii after hub spiral or temporary spiral construction had begun.

O6.1.1.4 Secondary frames

The secondary frames of *M. duodecimspinosa* were built relatively later in radius construction than in *L. mariana* (TET) and *Philoponella vicina* (UL) (Eberhard 1990*a*). Tertiary frames (a frame attached at one end to a secondary frame, and presumably built with similar behavior) did not occur in *M. duodecimspinosa* webs, but were common in the orbs of some other araneid species such as *Allocyclosa bifurca* and *Cyclosa* spp. (arrows in Fig. 7.41c). Occasionally the final radius laid by *M. duodecimspinosa* in a sector with a secondary frame was not attached to the secondary frame; instead the spider moved to the end of the secondary frame and beyond, and attached the new radius to the adjacent primary frame line (Fig. 6.8). At least in *L. argyra*, this "going around a corner" sometimes resulted in the spider moving closer to the hub and thus slackening the new radial line (a in Fig. 6.8), and the spider sometimes appeared to compensate for the reduced tension by making a second attachment farther along the frame before breaking the new radius and reeling it up as she returned to the hub (Fig. 6.8c).

O6.1.1.5 Temporary spiral and tertiary radii

The distances between radii were small enough in M. duodecimspinosa orbs that the spider could reach directly from one radius to the next without releasing temporary spiral, even in the outer part of the orb. Thus the spider traveled in an approximately spiral path while building the temporary spiral. In A. diadematus, as in most orb weavers, the spider moved inward and then back outward as she laid each segment of temporary spiral in the outer part of her orb (e.g., Figs. 6.1, 6.23; Zschokke and Vollrath 1995a; Zschokke 1996).

Tertiary radii, which are built when the spider added another radius during temporary spiral construction which originated where she interrupted the temporary spiral, were built occasionally by *A diadematus* (Peters 1937*a*, 1937*b*), but were never observed in *M. duodecimspinosa*. They were more common in other typical orb weavers such as *Zygiella x-notata* (AR) (Le Guelte 1966) and *Uloborus diversus* (UL) (Eberhard 1972), and abundant in others such as *Nephila* spp. (NE) (Fig. 4.4), *Enacrosoma anomala* (AR) (Fig. 3.42), and *Cyrtophora citricola* (AR) (Fig. 1.7, section O6.3.5).

O6.1.1.6 Sticky spiral: translating cues into behavior

A large number of variables are known to affect the decisions that a spider made as she spiraled inward and attached the sticky line to each radius that she crossed (section 7.3); but the behavioral mechanisms by which these stimuli are converted into how she moved particular legs and where she grasped lines have hardly been studied. These conversions are nevertheless key to understanding how sticky spiral spacing is determined (and, for that matter, other aspects of web design). Two decisions likely to be important are 1) where tarsus oIII and tarsus oIV grip the radius, and 2) choosing where, between these two tarsi, the spinnerets touch the radius to make the attachment (time 0 in Fig. O6.1). One study documented the importance of where grips occurred. The site where leg oIV of *M. duodecimspinosa* grasped the radius differed when the spider was above vs. below the hub, and near the hub vs. far from it), and these variations correlated with the attachment sites (sticky spiral spacing) (Eberhard and Hesselberg 2012). Either the site grasped by oIII or the site where the spinnerets touched the radius with respect to the sites leg oIII and oIV was also probably important, because variations in spacing were only partially explained by the site grasped by oIV (Eberhard and Hesselberg 2012).

Almost nothing is known for any other species, though isolated examples show that variation exists. In *Gasteracantha cancriformis* (AR) the sites on r_n that were gripped by legs oIII and oIV were sometimes so close together that the portion of the abdomen bearing the spinnerets barely fit between them. In this case the two leg positions must have determined the attachment site, but on other occasions the legs were farther apart (as in *M. duodecimspinosa*, both during hub loop construction and during sticky spiral construction) (during hub construction the spinnerets touched r_n much nearer to oIV than to oIII; but they tended to touch near the midpoint between legs oIII and oIV during sticky spiral construction) (WE). In *Zosis geniculata* (UL), attachments of the sticky spiral were nearly perfectly centered between the points where legs oIII and oIV grasped the radius (arguing for the importance of grasping sites determining attachment sites), but during both the attachment of a new radius to the frame and the attachment of the hub spiral to a radius attachments tended to be closer to the point grasped by leg oIII than leg oIV (WE).

The sites grasped by legs oIII and oIV may have been affected by the coordination between their movements and those of other legs in *Z. geniculata* during sticky spiral construction. Leg oI tapped laterally to locate the inner loop at the same time that legs oII and oIII slowly walked “hand over hand” outward along the radius, and the coordination between the steps of oII and oIII and the moment when oI touched the inner loop varied. In general, as soon as oI contacted the inner loop, oII and oIII ceased taking new steps, and oII moved toward the next radius (r_n in Fig. 6.24). In some cases, oIII was grasping a site on the hub side of oII when oI contact occurred, and in these cases it remained in this position as the spider turned to attach the sticky line. But when oIII was beyond oII when oI contact occurred, or when it had already begun a step and then finished making this step, it grasped r_n beyond the site being held by oII as the spider turned to attach the sticky line (WE). Differences in the coordination between the oII and oIII stepping movements and the oI contact may correlate with variations in sticky spiral spacing, but the measurements needed to test this idea have yet to be made.

The number of times that legs IV pulled out additional sticky line from the spinnerets varied in different portions of the orb in *M. duodecimspinosa*. Near the outer edge the spider pulled a mean of 11.1 ± 0.3 times (counting the large, final pull preceding the attachment (time 0 in Fig. O6.1; see also times 2.00, 4.44 and 4.89 for other pulls). In the last two loops of this same web while the spider was moving in the same direction (upward) in the same sector (7:00 – 11:30), the mean was much lower (1.0 ± 0) (WE). *Gasteracantha cancriformis* (AR) showed higher values (also for loops in the same sector going in the same direction): when the sticky spiral was about half complete, the spider made a mean of 12.9 ± 1.5 pulls; in the last two loops, she made 3.9 ± 1.2 pulls (WE).

Many patterns of this sort probably remain to be discovered in *M. duodecimspinosa* and *A. diadematus*, as well as other species.

O6.1.2 Orb web repair

“Shoring up” repairs which involved adding non-sticky lines to damaged sectors soon after the damage occurred, have been described in *Araneus diadematus* (Peters 1933*a*, 1933*b*), *Zygiella x-notata* (Wiehle 1927), *Argiope argentata* (Robinson and Olazarri 1971, *Nephila* spp (Robinson and Mirick 1971; Robinson and Robinson 1973*a*) and *Uloborus diversus* (Eberhard 1972). As the name implies, these repairs occur soon after the damage occurred, and apparently functioned to protect the rest of the orb from further damage. Generally the spider attached non-sticky drag lines to other non-sticky lines in the damaged area, in effect reconnecting broken lines, though not necessarily as they had been before. The simplest cases involved reconnecting the ends of a single broken radius (Fig. 6.17a), but repairs were more elaborate when the hole was larger (Fig. 6.17b). When shoring up a broken frame line which had been under high tension, *U. diversus* laid several drag lines back and forth across the hole, gradually attaching her drag line farther and farther from the hole and cinching up the tension on the frame line (WE).

O6.1.3 Web removal and recycling

Building on the pioneering observations of Nielsen (1932) on *Cyclosa conica* (AR), Carico (1986) showed that the process of destroying and ingesting an orb constituted the first step in building the next one. Typically, the spider removed the radial, sticky spiral, and hub lines, leaving the frame and anchor lines and a few new radial lines that were laid in this process intact. The old web was broken, packed together, and ingested sector by sector in snow plow–like sequences. Starting at the hub, the spider moved outward, breaking, packing together and ingesting radii and sticky spiral lines, laying some of the new radial lines that would be included in the next orb in the process (Fig. 6.20). Removal was generally more or less leisurely, lasting from 35 to 55 min in the araneid *Neoscona hentzii*; *Allocyclosa bifurca* (AR) and *Leucauge mariana* (TET) made rapid “snow plow” removals in the moments immediately preceding a rain storm (WE). Carico observed snow plow recycling behavior in the araneids *Cyclosa turbinata, Neoscona crucifera* (= *hentzi*), *Micrathena gracilis, M. sagittata, Argiope fasciata, A. aurantia, Metepeira labyrinthea, Nuctenea cornutus*, and *Mangora* sp., and speculated that it occurs in the majority of orb weavers.

He also observed a second, much more rapid “window shade” type of orb removal in *Acacesia hamata*, a species which makes especially large investments in large, very dense nocturnal orbs (Fig. 3.5). The spider gathered up the entire vertical orb in one operation which took as little as 60 s: she broke the two frame lines that were attached to the lowermost anchor lines in the web, collapsing the sticky mass of spiral and radial lines upward against the upper, more or less horizontal frame line, and then rolled up and ingested this compound line. Rapid removal occurred at dawn (all of the individuals that were observed in this context), or when it began to rain (most of the individuals observed). Sprinkling field webs with water at night induced window shade removal in one third of the cases. Window shade removal also occurred in the araneids *Verrucosa arenata, Eustala anastera,* the ladder web spider *Scoloderus tuberculifer*, and in *Neoscona hentzi*. The Australian araneid *Poltys noblei* also removed its dense, nocturnal web rapidly at dawn, but with a still different technique (Smith 2006).

Rapid removal probably enables the spider to reduce losses from rain (and also dew at dawn?) (Fig. 8.10), and could also reduce predation by visual predators, which begin to be active at dawn (Carico 1986). One disadvantage of rapid removal is that it removes all but two connections with the substrate, and may thus be costly in terms of the subsequent effort and material needed to locate attachment sites (Carico 1986).

As is often the case with spider webs, there are complications in this simple story of admirable recycling efficiency. In the first place, not all spiders that could recycle silk do so. Paradoxical failures to reingest old webs been seen in the araneids *Mycenogea lemniscata* (Carico 1986) and *Cyrtophora moluccensis* (Lubin 1973), the theridiids *Parasteatoda* (= *Achaearanea*) *tepidariorum* (Turnbull 1964) and *Latrodectus* spp. (Eberhard et al. 2008*b*), the nephilid *Nephila clavipes* (one mature female left most of her previous orb intact when she moved to a new web site about 1 m away) (WE). *Micrathena duodecimspinosa* (AR) also failed to ingest accumulations of silk during exploration and the initial stages of orb construction (WE). *Uloborus* and *Philoponella* (UL) sometimes do (Lubin et al. 1982) and sometimes do not ingest old silk (Eberhard 1972), while *Hyptiotes paradoxus* (UL) and *Zosis geniculata* (UL) actively discard it (Marples and Marples 1937, WE).

The possible metabolic cost of packing silk lines together prior to ingestion does not explain these omissions: *M. lemniscata* and *Z. geniculata* collapsed their entire horizontal orbs so they resembled small balls of cotton, but then dropped them (Carico 1986, WE). The uloborid *U. diversus* carefully packed the fluff from early lines into a tight ball at the proto-hub, then flicked it away (Eberhard 1972). The funnel web weavers *Tengella radiata* (Tengellidae) (WE) and the *Aglaoctenus castaneus* (Lycosidae) (Eberhard & Hazzi 2017) sometimes had remnants of an old sheet below the new one in the field (perhaps in these cases the frequently substantial accumulation of detritus on the old lines made reingestion impractical).

O6.2 Details of the movements of *M. duodecimspinosa*

This appendix describes "lower level," finer details of the movements of the body and legs of mature females of the araneid *Micrathena duodceimspinosa* during orb construction. These highly coordinated leg movements, nearly all of which were omitted in the text, constitute the behavioral mechanisms by which the higher-level operations described in section 6.4 were executed. They thus constitute the "atoms" or basal units of building behavior in this species. Previous descriptions of orb construction have seldom included details of this sort, and there are few data for *M. duodecimspinosa*. Taxonomic comparisons, as in Appendix O6.3 for higher level behavior patterns, are thus not possible. The nearly complete lack of previous descriptions does not imply either a lack of importance for the spider, nor a lack of possibly interesting consequences of the observations (e.g. their usefulness as taxonomic characters), but simply a lack of research effort.

The accounts below are only preliminary in the sense that they only take into account the variations in the details according to crude, preliminary variables, such as execution during temporary spiral construction rather than sticky spiral construction, or behavior while the spider is above as opposed to below the hub. They are also based on video recordings of only 1-5 different spiders (different numbers for different stages of construction), and include only very incomplete attempts to describe variations. Further analyses will almost certainly reveal a rich array of adaptive variation in the behavioral details that orb weavers use to accomplish different tasks in different contexts. The objective of including these incomplete descriptions is to highlight their diversity, and to provide a base for future comparisons with the behavior of species in other taxonomic groups.

O6.2.1 Exploration and establishing early lines

O6.2.1.1 Break and reel behavior

Movements used by *M. duodecimspinosa* in exploration are illustrated in Fig. 6.4. "Break and reel" or "living bridge" movements (Marples and Marples 1937) and the associated reconnections of the broken lines (outlined in Fig. 6.4b) involve particularly precise leg coordination and attachments. They were performed quickly and smoothly, but they involve a complex "juggling" act by the spider, in which she accomplished several functions more or less simultaneously: sustain her own weight; manage not to lose the loose ends of broken lines that were floating in the air; and hold the line to which she makes each attachment of her drag line tight at the appropriate sites. All of this was done "blind", without seeing the lines.

Break and reel behavior is crucial to solving an important but previously unappreciated problem. A spider obviously did not know beforehand what attachment points she would encounter as she explored a site. She also always produced a drag line continually as she moved about, attaching it to many of the the objects she encountered and also to other she had already produced. The inevitable result was that the spider produced lines during exploration that were in inappropriate positions for the orb. Break and reel behavior allowed her to shift the positions of lines (Fig. 6.4c,d); she also discarded lines entirely by simply releasing the line that she was reeling in, and then climbing back her dragline to the last attachment). For instance, she moved an attachment of a radial line sideways along a pre-existing line during exploration (Fig. 6.8a) executing the following movements. While holding the pre-existing line, she brought the radius to her mouth with her palps and broke it, then moved sideways along the pre-existing line (legs I and II on the leading side followed each other). Then she re-attached the radial line by grasping the pre-existing line with her trailing leg III (which followed ipsilateral II), and then with ipsilateral leg I; they held it against her spinnerets as she attached her dragline. At the same time, she explored rearward with her leading leg I and perhaps II to locate and grasp her dragline, and the anterior portion of her body turned away from the pre-existing line, bringing her posterior end closer to it to make the attachment. After attaching her dragline to the previous line, she immediately broke the dragline she had just attached, and began to return along this line, reeling up the old line with legs I and II and packing together the loose line with legs III and perhaps her palps. Throughout the process, she simultaneously sustained her own weight by grips on both the dragline and the pre-existing line with these and other legs.

Leg and spinneret movements of similar complexity occurred in other contexts during exploration and other stages of orb construction, but they have received so little attention that a useful discussion of which behavioral "atoms" occur in which order in these behavior patterns must be postponed until a new generation of studies becomes available at this level of detail.

O6.2.1.2 "Fishing" by floating lines on the breeze

The spider discovered and linked possible attachment sites for her web by "fishing" for them. The first step was to attach her dragline to the substrate (or more commonly, to a short line already attached to the substrate), descend a short distance, and allow the breeze to pull up to a meter or more of additional new line from her spinnerets (Fig. 6.4a). The distal tip of the line was apparently very thin (as is typical in other spiders – see Savory 1952; Eberhard 1987*b*); like Savory, I was unable to see the tip of the line even under the most favorable lighting conditions. In the giant orb weaver *Nephila pilipes* (= *maculata*), this line emerged from the posterior lateral spinnerets and its tip was a cluster of fine lines that floated freely on the breeze (Hingston 1922a). After a little of the thin line had been pulled, a thicker, visible line was attached to it and began to be pulled out (the descriptions below refer to this subapical, visible portion of the line).

Air movements were typically more or less horizontal, but when the breeze was weak and its direction changed repeatedly the fishing line sometimes also moved vertically. The distal portion of the line generally swung or flipped slowly back and forth in the breeze. When a fishing line became snagged or tangled, it was generally on an object that was more or less directly downwind and at about the same height as the spider. It appeared that the spider generally did not sense the moment that her the line contacted an object, and gave no immediate response when the line snagged on a motionless object, or when I snagged it and held it still. If the object moved and pulled the line tight even briefly, however, she immediately pulled on the line. Sometimes a spider paid out a meter or more of fishing line, and then waited for up to a minute or more.

Eventually the spider reeled in the line, whether or not it had snagged on an object. If the tip was still free, she reeled it in entirely, forming a ball of fluff which she attached to the line she was on, and then, often after a pause of up to several minutes, released another fishing line (perhaps she was waiting for a change in wind direction?). If the fishing line had snagged on an object, the spider pulled the line more or less tight, and then (but not always) walked along it toward the object. She usually broke and reeled this line (Fig. 6.4b) as she went, but occasionally she added her dragline to it. Frequently she released much more line than she reeled in when she began to move toward the new object, causing her (and the line) to sag substantially downward (up to 1 m) (Fig. 6.4b). As she approached the new object, she reeled in more than she released, and thus moved upward; often she arrived at the object from nearly directly below. Both *A. diadematus* (AR) and *Uloborus diversus* (UL) apparently performed similar (though smaller) sags during exploration (Eberhard 1972; Zschokke 1996). These sags swept the line downward, and may serve to check for objects in the space below that could interfere with an orb (Zschokke 1996); experiments are needed to test this idea.

Occasionally the fishing line was only weakly entangled, and broke free as the spider approached. When this happened, she climbed her dragline back to her original site, reeling up the line as she went, and resumed fishing. When the entanglement was strong enough to support her weight she usually reached the new object, but sometimes she "rejected" the object, cutting the line and producing a new fishing line; some rejected objects were close to the original fishing site, and thus were not useful anchor points for a a new web, experiments will be needed to understand rejection.

When the spider reached a new, nearby object, she sometimes walked up to a meter or more along it or along other objects that were connected to it, and then again resumed fishing; perhaps the nearness of the object signaled a lack of a clear, open space downwind from her original site, and thus the need to move somewhere else. Mechanisms by which a spider might sense the distance to an object include the rate at which she swung from side to side when on the line which had snagged the object (lower when the line is longer), the extensibility in the line when she pulls on it (more extensible when the line is longer), or simply by how far she walked to reach the new object.

Eventually, sometimes on her very first try but more often after 5-10 tries, the spider snagged a fishing line on an appropriately distant object (approximately 1-2 m away), establishing the more or less horizontal line that would form part of the uppermost frame line of her orb. She then continued to fish from this line, sometimes near the original attachment site, sometimes nearer the center of the new line. The details of this fishing behavior were similar except that the rate of successfully snagging a useful object was lower, at least in the relatively open semi-natural sites with only sparse potential attachment sites where I observed this behavior (in nature, finding sites sufficiently open may more often be a problem than finding attachment sites). One additional fishing tactic was to descend at the end of a dragline attached to the bridge line or by breaking the bridge line and sagging it just before paying out fishing line (Fig. 6.4b). Such descents enabled spiders to fish for a third object farther below the bridge line.

Some spiders spent up to an hour or more fishing for a third anchor site. Sometimes, after a spider had made repeated fishing attempts it became clear what she was attempting to do, and I had the unique thrill of actively participating in building an orb. I grasped the fishing line, and carefully moved it (without pulling on it) so its distal portion tangled on an object that was appropriately distant and below the bridge line. The spider accepted my help in 7 of 7 tries: she moved to the new object, attached her drag line to it, and immediately ceased fishing and proceeded to the next stages of orb construction (Fig. 6.5).

The general lack of observations of web initiation under natural conditions in other orb weavers precludes judging how frequently other spiders experience problems in finding attachment sites. It is possible that *M. duodecismspinosa* is unusually reliant on air movements.

Several species (e.g. *Araneus diadematus, Zygiella x-notata, Leucauge argyra, Uloborus diversus*) built in closed cages with no air movement. There are descriptions of simple descents to find a third attachment point after having established a more or less horizontal bridge line (including the variant behavior of swinging during such a descent to allow the spider to make the web non-vertical). Gravity and walking along the substrate possibly play larger roles in other species.

O6.2.1.3 Snubbing attachments to the substrate

The spider often "snubbed" attachments to the substrate by walking to or just over the edge of an object and attaching her drag line on the far side of the object (caption of Fig. 6.5). Sometimes, when the object was thin, like a small twig, the spider walked all the way around it before making the attachment disc (section 5.3.5). Snubbing appears not to have been described in previous publications, but I have also seen it in several species, including *Uloborus diversus,* (UL), *Philoponella vicina* (UL), and *Nephila clavipes* (NE), so it is probably widespread.

O6.2.1.4 Probable tension adjustments

Probable tension adjustments occurred repeatedly during exploration and during the very first stages of orb construction. Changes in tensions on a line during construction could be noted by watching the angle the line made with other lines: an increase in tension pulled the other line farther out of line. One inadvertent "experiment" permitted me to observe *Micrathena duodecimspinosa* making such an adjustment. The first horizontal line was attached to the tip of a leaf, and the leaf bent progressively farther toward her when she tightened this line. Tension adjustments also included cinching up the first frame line by reeling it in (Fig. 6.5d), then of immediately loosening it by lowering the tension on the first primary radius as she established the definitive hub (Fig. 6.5d).

O6.2.1.5 Following behavior

"Following" behavior, in which a one leg grasped the line near the point being held by the immediately anterior ipsilateral leg just before this more anterior leg moved forward (section 2.4.2.1), occurred during at least some portions of exploration (section O6.2.1.1).

O6.2.1.6 Sliding tarsus IV along the dragline

Wherever the spider moved while producing non-sticky line, she almost always grasped her dragline with one tarsus IV. This leg remained extended posteriorly without taking steps, and slid along the dragline as the spider moved (Fig. 6.4). Presumably the line slid under the median tarsal claw, and/or across the modified accessory setae (Fig. 2.16). This contact continued when the dragline was attached to another line, at which time the opposite leg IV and its ipsilateral III grasped the line to which the attachment was being made, and held it against the spider's spinnerets (Fig. 6.4, see section 2.4.3). Holding the dragline continuously with one tarsus and sliding it through tarsal claw IV was widespread but not universal among web building spiders (Eberhard 1986*c*), and may be a synapomorphy of Orbicularia. Probably this behavior functions to increase the spider's control over the position or tension of her dragline, but there are no tests of this idea.

O6.2.1.7 Exploratory descents

Occionally a spider attached her drag line to an aerial line and then allowed herself to fall, holding her drag line with one IV to sustain her weight and waving her other legs in an apparent search for objects to which to attach. If she failed to contact anything (nd sometimes even after making a contact), she reascended her drag line, pulling herself up with legs I and II and packing the loose line together with legs III.

O6.2.2 Secondary radii and frame lines

During secondary radius construction the upper leg I (and sometimes ipsilateral leg II) grasped the radius or the radii on the upper side of the sector into which the new radius was about to be laid, and legs I and II made repeated quick, medially directed tapping or slapping movements in the air in the open sector just below, presumably to confirm that there was no radius already present. When nearly all radii has been built, the spider sometimes rotated slowly through up to 360º, facing away from the hub and repeatedly grasping and releasing adjcent pairs of radii with her legs I and II and sometimes slapping in the spaces between them. Presumably she was searching for over-sized sectors into which to insert another radius, using the separation between her legs as she grasped pairs of radii to measure the angles between them. These apparent explorations sometimes resulted in placement of one or two additional radii, but eventually gave way to initiation of the hub spiral (in this species. Similar apparenently exploratory movements with legs I nd II to sense over-sized sectors occurred in *A. diadematus* (AR) (Peters 1937*a*, 1937*b*) and *Leucauge mariana* (TET) (WE); those in nephilids and uloborids differed (section O6.3.2).

While walking away from the hub toward the frame to lay a radius, the spider held one leg III somewhat extended vertically, and appeared to slide the tip of the tarsus of this leg along the radius, with the exit radius thus being held slightly away from the spider's body. At the same time the tarsus of one leg IV held her dragline, which also slid through the tarsus as she walked. Leg positions when attaching her dragline to the frame were standard: the spider held the frame with ipsilateral legs III and IV on either side of the attachment point, and the new. provisional radial line with her other leg IV.

O6.2.3 Hub construction

Hub construction (Fig. O6.4) began at or near the end of secondary radius construction. Legs oIII and oIV held the radius on either side of the point where the spinnerets made each attachment of the hub line to a radius. The spider's outer legs followed each other in both space and time (see Fig. 6.12). They moved in the following order after each attachment: oIII (to the line held by oII); oII (to the line held by oI) and oIV (to the line held by oIII); and then oI. In each case, the more anterior leg did not move forward until the trailing leg had grasped the radius. Leg iIII was held immobile at the very center of the hub during construction of the first loop of hub spiral (section 6.3.3.4), perhaps to serve as a point of reference to allow the spider to make a more less circular first loop. The spider released this hold with iIII while building subsequent hub loops, and this leg III subsequently moved only occasionally, apparently functioning only to support her weight. The spider apparently used information from her palps and perhaps leg oIII regarding the site of the first loop to achieve regular spacing between hub loops. Her palps consistently tapped and apparently held the first hub loop while she built the second loop, and leg oIII appeared to slide inward along the radius to contact the outer hub loop just an instant before the attachment was made. If oIII consistently contacted the outer loop (as appeared to be the case in some video recordings) (as was confirmed to occur in *Nephila clavipes*) (section O6.3.4.2), this leg probably provided information on the location of the outer hub loop.

Later in hub construction the spider's inner leg I or II consistently grasped the outer hub loop, and later still iI and iII often moved hand-over-hand along this loop. Each leg appeared to explore independently for the next site to grasp, and iII did not follow iI. Leg iIV played no direct role in attachments; the tip of its tarsus was sometimes in the vicinity an attachments as it was being made, but in other cases it lagged far behind and moved less than once/attachment. This leg was thus apparently used to support the spider's weight, rather to manage the drag line as typically occurred in attachments made in other contexts (Eberhard 1982). The palps often contacted the outer hub loop several segments ahead of the attachment radius; perhaps they were used for general, long-range guidance while oIII was used for immediate decisions regarding attachment sites.

O6.2.4 Temporary spiral construction

Leg positions at the moment each segment of the temporary spiral was attached to a radius were relatively consistent. Legs oIII and oIV held the radius on either side of the point on the radius to which the temporary spiral was being attached, while leg iIV held the dragline (the new segment of temporary spiral). Just prior to making an attachment, the spider waved leg oI to search for and then grasp the radius to which the temporary spiral would be attached (the next radius beyond that to which the previous attachment was made). In the outer part of the orb, the spider then turned to face more or less away from the hub and moved outward, but maintained a grip on the previous loop of tsp with leg iI or iII. First leg oII and then leg oIII followed oI in grasping this next radius. Just before attaching the new segment of tsp, the spider turned approximately 180° to face inward.

As with the radii, the temporary spiral lines were under tension. In some species the temporary spiral pulled them out of straight lines and these displacements showed consistent patterns. When the angle bounded by two adjacent radii was relatively large (e.g. the angles between radii 0_y and 54, 0_x and 48, and 0_w and 49 in Fig. 6.10), the radii were displaced toward each other. The direction in which the spider was moving as she built the temporary spiral loop or loops that pulled the radii out of line this way did not appear to influence the direction of the curve. For instance, radius 0_y in Fig. 6.10 was pulled upward as the spider ascended in the orb, but 0w was pulled upward as she descended.

O6.2.5 Sticky spiral construction

The movements of some legs during sticky spiral construction were intelligible in terms of their probable functions: 1) to inform the spider of the position of nearby radii and the inner loop of sticky spiral that were already present in her web; 2) to guide the movements of other legs; 3) to bring lines to the spinnerets in order to attach the new line she was spinning; 4) to sustain the spider's weight in the web; and 5) to hold the spider's body away from the orb's plane in nearly vertical webs, in which there was the possibility of contacting web lines directly under the spider. As was documented long ago by Fabre (1917) and Hingston (1920), the temporal coordination of some leg movements and the behavior of attaching the sticky spiral to the radius suggested that several types of movements functioned to locate particular lines in the web (the radius, the inner loop of sticky spiral).

"Inner loop localization behavior", in which one leg tapped or extended toward the inner loop of sticky spiral already in place until it touched this line, functioned to guide sticky spiral construction (section 7.3). Direct observations confirmed this function. As soon as the leg contacted the inner loop, the spider ceased this behavior, and turned to make the attachment. She held the radius (r_n in Figs. 6.24, O6.1 – O6.3) with her legs oIII and oIV on either side of the point where she touched her spinnerets to the radius to attach the sticky line. Inner loop localization by *M. duodecimspinosa* was atypical for araneids. Leg oIV rather than oI performed inner loop localization. After leg oIII had moved forward to grasp r_n, leg oIV moved forward and contacted the radius just outside of the point where oIII was holding it, then moved quickly outward (dorsally). This movement often lasted only on the order of 0.03 s; it was obvious in video recordings, but was often difficult to distinguish with the naked eye. When the leg contacted the inner loop, it immediately moved ventrally to grasp the radius by flexing slightly (ventrally); the tip of the tarsus often held the radius at or very near the junction with the radius. Leg oI seldom tapped laterally, and even more seldom touched the inner loop; leg oII also only occasionally and erratically touched the inner loop. This inner loop localization behavior is undoubtedly secondarily derived, because leg oI is used other araneids, including *M. schreibersi* and *M. gracilis*; in *M. horrida, M. sexspinosa* leg oI is used near the outer edge of the web but leg oIV is used near the hub (where lines are closer together) (Eberhard 1982). As in other contexts, some legs followed others (section 2.4.2.1, Table O2.2).

Aside from inner loop localization, there were several other general patterns of leg movements in araneids (Fig. O6.1), tetragnathids (Fig. O6.2), and nephilids (Fig. O6.3). The legs that held the radius against the spinnerets on either side of the attachment point were the same (oIII and oIV) and the current segment of sticky spiral was pushed anteriorly and ventally just before the moment of attachment with the same leg (iIV). This pushing movement almost certainly resulted in additional sticky line being drawn from the spider's spinnerets, and thus in lowering the tension on the new segment of the highly extensible sticky spiral being laid; this probably improved its ability to retain prey (section 3.3.3.1). Pushing with leg iIV displaced the sticky spiral line emerging from the flagelliform and aggregate gland spigots on the posterior lateral spinnerets anteriorly, bringing it into the vicinity of the piriform spigots on the anterior lateral spinnerets; this may have facilitated use of the piriform silk to make the attachment. In *M. duodecispinosa* pushing with leg iIV was omitted in the interior portion of the orb, where the distances between radii were small; leg iIV was apparently used only for support, as it held radii or hub lines and moved only infrequently.

Although there are no careful studies of variations in leg movements, they clearly varied substantially (Fig. 6.24). Table O6.3 summarizes of variations in both the legs' movements and their functions when the spider was above and below the hub in the outer portion of the orb. The path of the spider's body also varied as she moved inward and back outward to make each attachment according to the distance to the outer loop of temporary spiral, and her distance from the hub (Fig. 6.25). The numbers of steps/attachment decreased for some legs but not for others when she was nearer the hub (Table O6.3). Differences in displacements of web lines when different tarsi grasped them also suggested substantial variations in their use in sustaining the spider's weight in different parts of the web (Fig. 6.24, Table O6.3). The rear legs sustained most of the spider's weight as she descended, while her anterior legs sustained most of her weight as she climbed (Fig. 6.24). Similar variations can be deduced from figures of other species such as *A. diadematus* (Mayer 1952).

Presumably the spinnerets of *M. duodecispinosa* performed movements similar to those observed in *Nephila clavipes* when the spider attached the sticky spiral (section O6.3.6.3), but they were too small to discern behavioral details.

Spiders broke temporary spiral segments during sticky spiral construction (section 6.3.5.1). To break a temporary spiral line, the spider first grasped it with leg oIII soon after she made an attachment of the sticky spiral; then she pulled it toward her mouth with her palps, and she broke it as she moved toward the next radius. The temporary spiral line broke without sign of being stressed: the two broken ends simply fell away, and the short, lax lines curled up spontaneously where they were attached to the two radii. Breaking a segment of temporary spiral took only about 0.1 s.

O6.2.6 Hub modification

No detailed study of how the central portion of the hub is removed is available. The events in one video recording of an adult female *M. duodecimspinosa* are desribed in Fig. 6.16); this sequence resembled, at least in general terms, the behavior of nine other individuals that were also filmed. Legs I and II made many small grasping and regrasping movements as the spider arrived at the hub after finishing the sticky spiral, until they eventually spanned the central portion of the hub and brought the spider's mouth into position at the upper end of the central area. Here she began to break and ingest lines by bringing them to her mouth with legs II and III. These legs also repeatedly grasped and regrasped different lines as if exploring to find them. The spider gradually eased downward as she removed lines, keeping her legs I in the same positions or only shifting them slightly. She broke portions of the innermost loop of hub spiral, and it sagged against the second loop, forming the innermost hub loop in the finished web. She initiated a new dragline just before beginning to break lines, dabbing her abdomen repeatedly to a radius held by ipsilateral legs III and IV just above the central area. She then flexed her abdomen dorsally, away from the web until, at the end of hub removal, she moved her body rearward and made another dragline attachment just above the upper end of the hub hole, and assumed her web monitoring position, pulling the edges of the hole she had created toward each other (see Fig. 3.37e,h-j).

Precision is crucial in breaking the lines in the central area of the hub, because a mistake could affect the physical integrity of the hub and the functionality of the web. Probably the crucial stage in guaranteeing that the appropriate lines were broken and not others was the original alignment of the spider's body, which she appeared to accomplished by positioning her legs I so that they spanned the hub more or less symmetrically (Fig. 6.16); this positioned her mouth area near the center of the hub. The repeated "regrasping" behavior of her legs (especially legs I) may have represented small exploratory movements that allowed the spider to locate the appropriate hub loops and thus allow her to position her body at the center of the hub, but further study is needed to test this idea.

After she finished making the hub hole, the spider often jerked the web one or more times. In a video recording of a similar jerk performed by a close relative, *M*. sp. nr. *lucasi* (AR), was produced by a quick dorsal flick of her abdomen. The jerks seem designed to cause any immobile object in the web to swing, thus generating vibrations that would allow the spider to sense its presence.

Very little is known regarding hub modification behavior in other species, but there may be taxonomic differences in some of details. In one video recording, *Gasteracantha cancriformis* (AR) positioned herself similarly, spanning the central portion of the hub with her legs I and II prior to beginning to remove the center; but she also simultaneously performed several sharp jerks with her legs as she was doing so, perhaps to gather stimuli from her web.

O6.3 Comparisons with other taxa of orb weavers

This appendix contrasts the building operations (and a few details of leg movements) that are performed by members of other orb-weaving taxa other than *M. duodecimspinosa* and *A. diadematus* to accomplish similar objectives (build radii, frames, etc.). The observations of *Nephila clavipes* (NE), *Leucauge mariana* (TET), *Philoponella vicina* (UL), *Zosis geniculata* (UL), and *Gasteracantha cancriformis* (AR) for which no citations are given come from my own unpublished observations of adult females.

The descriptions here are simplified. As is inevitable, given the paucity of published data, lower level aspects of building behavior are especially poorly covered. I have mostly included only what seem to be major points of difference and similarity between groups, rather than giving complete accounts. The descriptions are thus even more typological than in the accounts above. I have also ignored inter-specific diversity in most groups. I will refer to *Micrathena duodecimspinosa* and *Araneus diadematus* described above as "typical araneids".

O6.3.1 Exploration and establishing early lines in other orb weavers

The previous descriptions of exploration by other araneid orb weavers, such as Hingston 1920 on *Neoscona nautica*, Hingston 1922a on *Nephila maculata*, Witt et al. 1968, Vollrath 1992 on *Araneus diadematus*, and Gregorič et al. 2011b on *Caerostris darwini*, and Eberhard 1972 on *Uloborus diversus* (UL), seem not to differ in any important way from those of *M. duodecimspinosa* (all details were not clear in some descriptions). The details of leg movements were also similar to those in other groups, as far as they are known.

It seems likely that at least some species, such as *Allocyclosa bifurca, Cyrtophora citricola,* judge the degree of rigidity of the sites to which lines are attached during exploration (section 7.19.3). One way to judge the rigidity of a supporting object could be to pause to rest on a line attached to it, to see whether wind causes it to move. This is a possible (though untested) explanation for the frequently long interruptions that often occur during the during the exploration stage in all of the species studied.

O6.3.2 Radii

O6.3.2.1 Other araneids and tetragnathids

The operations involved in laying a radius seem to be similar throughout araneids and tetragnathids to those of *M. duodecimspinosa* and *A. diadematus.* Minor variations included the following. There was some variation in the site where the radius was broken on the way back to the hub (Zschokke 2000b); *Cyrtophora* related genera differed slightly (Fig. O6.5); and *Caerostris darwini* doubled the radii in the upper but not the lower part of the orb (Gregorič et al. 2011b). Radii were mostly laid at "final angles" (the sector between a new radius and its exit radius seldom received any further radii) in the araneids *Zygiella x-notata* (Mayer 1952; Le Guelte 1966), *Micrathena gracilis* (Dugdale 1969), *Cyrtophora citricola* (Wiehle 1927, 1928; Kullmann 1958), and *Cyclosa conica* (König 1951), and the tetragnathid *Leucauge mariana* (WE). In one *C. conica* web, for instance, an additional radius was added to only 2 of 36 such sectors König 1951).

In contrast, the timing of hub loop construction with respect to secondary radius construction varied. In some species, such as the tetragnathid *Leucauge mariana*, radius construction was complete before hub loop construction began (Eberhard 1987*a*). In contrast, some araneids such as *Allocyclosa bifurca* initiated hub construction earlier, during the construction of up to the last 15-20% of the radii (WE).

In species in which hub construction occurred during radius construction, the spider interrupted hub loop construction to turn and face outward and grasp the two radii that she was holding with legs oI and oII with her two legs I. She then laid a new radius in the sector between these two radii, using one of these two radii (nearly always the upper of the two) as an exit radius and moving along the frame toward the other.

I know of only a single report for any species in these families of radii being added after sticky spiral construction was complete – in *Poltys noblei* (Smith 2006). Some symphytognathoids also add radii at this stage (below), but *P. noblei* differred in that these "extra" radii originated on other radii, rather than at the hub.

O6.3.2.2 *Nephila*

Secondary radius construction, which has been observed in several species of *Nephila*, including *madagascarensis, clavata, plumipes* and *clavipes*) (Hingston 1922a; Wiehle 1931; Shinkai 1982; Eberhard 1982, 1990*a*), as well as in other nephilids (including *Herennia,* and *Nephilengys*) (Eberhard 1982; Kuntner et al. 2008a), is unique (Fig. O6.5). The spider laid two new radii on each trip away from the hub. Usually each was attached at a different point on the frame line. Kuntner et al. 2008a report possible exceptions in *Nephila pilipes* and *Nephilengys papuana,* and *N. clavipes* made a single frame attachment to produce a doubled radius for exceptionally short radii (WE) This "two radii per trip" behavior may reduce by about half the energy and time spent in radius construction; this saving might be important because these spiders build relatively high numbers of radii (e.g., there were 112 at the outer edge of one *N. pilipes* web (Hingston 1922a; see also Fig. 4.4). Except for the very early radii (Eberhard 1990*a*), hub construction continued throughout radius construction in *N clavipes*; radii were apparently continuations of hub spiral lines.

Typical secondary radius construction by *N. clavipes* began when the spider interrupted hub construction to turned and face away from the hub. Leg oI waved or tapped in the space just beyond the radius that was being held by leg oII (the space between r_n and r_{n+1} in Fig. O6.8, where the next radii would be laid) (the "open sector" in the descriptions below). These movements were often followed by waving or tapping movements of oII in the same sector just after oI had grasped the next radius (the "leading edge" radius, which was on the far side of the sector into which the new radius would be placed). Presumably these tapping movements constituted searches to verify that there were no radial lines present in this space, and were thus analogous to the lateral slapping or tapping movements of legs oI and iI in *M. duodecimspinosa* (section O6.1.1.2). When the spider had turned her body more completely to face outward, leg iI (or iI and iII simultaneously) grasped the leading edge radius (r_{n+1} in Fig O6.8), while oI held the trailing edge radius (r_n). In sum, the spider only grasped the two radii bordering the sector (leading and trailing edge radii) simultaneously with her two legs I, as usually occurs in typical araneids (Fig. 6.4, section 6.3.3). late in the process. Presumably this means that cues guiding the decision whether or not to turn to add a radius (measurement of the angles between adjacent radii?) come from legs oI and oII in *Nephila*, rather than from the two legs I as in typical araneids. As in these groups, *N. clavipes* generally used the upper of the two as an exit radius to reach the frame (r_n in Fig. O6.8).

The spider slid the tarsus of one leg III along the exit radius for much of the way as she walked to its outer end, and the tarsus of one leg IV along the new dragline that she was laying as she went. When she reached the end of the exit radius, she moved laterally downward along the frame line and attached her drag line twice. Then she returned to the hub, walking along the first new radius (the dragline which she laid on the way out to the frame), laying the second new radius as she went. During the return trip to the hub, ipsilateral III and IV slid along this first new radial line. In at least some cases, the spider attached the second new radius to the first new radius (at 7 in Fig. O6.8) just short of its junction with the trailing edge radius at the edge of the hub (6 in Fig. O6.8), then resumed hub loop construction (e.g., attachments 8 and 9 to r_{n+1} in Fig. O6.8). The result was that both new radii appeared to originate on the outer hub loop (Fig. O6.8), a pattern also seen in *N. clavata* (Fig. 1 of Shinkai 1982). New radii were generally laid at final angles; neither the sector between the exit radius and the first of the two new radii nor the sector between the two new radii was subsequently divided in *N. madagascarensis* (Wiehle 1931) or *N. clavipes* (WE).

In most, if not all cases, the spider resumed circling in the same direction at the hub that she had been moving when she paused to build the new pair of radii. A typical sequence of leg movements as the spider reoriented herself at the hub and resumed hub construction was the following. When she arrived at the hub, she attached the second new radius as just described. Leg oI grasped lines far away, on the far side of the hub, and played no role in guiding the spider's reorientation. As she turned to continue the hub loop, leg oII waved in the hole where she had just laid the radii, and then grasped the leading edge radius (r_n). Simultaneously, oI grasped a radius a few radii ahead, but then moved back to wave and grasp the radius just beyond the leading edge radius (r_{n+1}). At the same time leg oIII waved several times in the next open sector, between r_n and r_{n+1}. Then both oIII and oIV simultaneously moved forward to grasp the leading edge radius (r_n) (possibly on either side of oII), oII advanced to the radius held by oI, and the normal sequence of hub construction following behavior began.

One variation seen occasionally in *N. clavipes* was for the spider to break the exit radius and reel it up as she moved away from the hub toward the frame. In these cases, she left a tangle of loose silk on the frame where she attached her drag line, then made a second attachment of her dragline, and returned to the hub. In these cases there was a net addition of only a single radius (two new lines added, one previous line removed); this behavior resembled frame construction in *Araneus diadematus* in which no radius was added (Zschokke 1996). A second probable variation (observed less certainly) was that sometimes very early in radius construction the two attachments of the new radial lines to the frame were relatively far apart, and the sector between the pair of new radii was so wide that subsequent radii were laid there.

O6.3.2.3 Uloborids

The uloborids *Uloborus diversus* (Eberhard 1972) and *Philoponella vicina* (Eberhard 1990*a*) differred substantially from araneoids in the early stages of construction (Fig. O6.6). One dramatic difference was that primary radius construction behavior was more stereotyped and tightly organized. In *P. vicina* (Eberhard 1990*a*) the initial exploration behavior changed more or less gradually into construction of several radial lines that converged on a central point (the "proto-hub") (Fig. 6.6), as in typical araneids. The spider eventually removed the small mass of fluff that had accumulated there as a result of the cut and reel behavior that occurred as the spider built and replaced the radial lines. But just before she removed this mass of silk ("proto-hub removal"), she first systematically modified the radii, partially or completely replacing them, and often added frame lines). The radii were modified in a strict sequence (Eberhard 1990*a*). For instance, in one web in which there radial lines a 1, 2, 3 5, 6 7, 9 and 10:00, the spider first modified the 9:00 radius and then, order, the radii at 7, 6, 5, 3, 2, 1 and 10:00. Each time a frame was added during radius modification, it was always laid so the exit radius was the "leading" or far side of the sector that the frame would span. Thus, for example, the exit on the 9:00 radius resulted in the construction of a frame connecting the 9:00 radius to the 10:00 radius; that on 7:00 resulted in a frame from 7:00 to 9:00., etc. The last few radius modifications preceding proto-hub replacement in *P. vicina* tended to involve smaller modifications of the web, such as a partial radius replacement rather than frame construction or a shift of the radius to the substrate (Eberhard 1990*a*). Finally, as the spider removed the mass of fluff during proto-hub removal, she reconnected the primary radii with a small circular line that became the center of the hub (Figs. 6.6). A mature female *Zosis geniculata* performed very similar behavior. She removed and ingested a mass of fluff, and reconnected the radial lines to form a small circular "proto-hub" after having built only approximately eight radii and some frames. This type of proto-hub removal may be exclusive to uloborids; it has never to my knowledge been reported in any araneoid.

There were two types of secondary radius construction in the two uloborids observed most carefully, *U. diversus* and *P. vicina*. The radii built (or renewed) during frame construction were laid using break and reel behavior, as in araneids (section 6.3.3.2), and no hub lines were built between one radius construction and the next. But after proto-hub removal, all secondary radii were doubled, and the spider laid hub spiral between constructing one radius and the next; the hub spiral was thus continuous with the radii.

There were three apparent differences between the construction of frames and early radii preceeding proto-hub removal in uloborids when compared with typical araneoid behavior: *a*) the concentration of all or nearly all frame construction in this early stage of construction; *b*) the strict sequence of radius modification and frame construction; and *c*) the consistent use of the radius on the leading side of the sector in which the new radius is laid as an exit radius (and the use of the leading edge radius as the exit during construction of radii following proto-hub removal). Both *a* and *b* have been seen in all uloborid orb weavers observed in detail (two *Uloborus*, two *Philoponella*, and one *Zosis* species – Eberhard 1990*a*). None of the three traits has been reported for an araneoid; all three probably represent taxonomically informative traits, though trait polarities (derived vs. ancestral) are not known. The lack of evidence in aranoids is not easy to evaluate, however, because lack of mention of relatively subtle behavior patterns, such as early frame construction and strict ordering of frame construction (*a* and *b*), does not necessarily mean that the behavior is absent. I judge from direct observations, however, that neither *a* nor *b* occurs in *M. duodecimspinosa* (AR), *Leucauge mariana* (TET), or *Nephila clavipes* (NE) (Eberhard 1990*a*, WE). The long history of observations of *Araneus diadematus*, without any reports of either trait, indicates that *a* and *b* are also absent in this species.

Araneids appear not use the leading radius as an exit (*c*), however, because they tend to use the uppermost of the two radii bordering the sector (sections 6.3.3.2, O6.1.1.5.2). A possible reason that uloborids used the leading edge radius as an exit is that it aided the spider in continuing to turn in the same direction (clockwise or counter-clockwise) when she resumed construction of the hub; this consistency allows the spider to avoid turnbacks in the hub loops, and increases her access to other portions of her orb.

A further major difference in uloborids was that the radial line laid as the spider moved from the hub to the frame was not broken and replaced when she returned to the hub during secondary radius construction (e.g., Fig. 6.5h,i,k); instead it was left in place, and the radius was doubled (Eberhard 1972, 1982).

An additional, less certain difference was that at least the two best studied uloborid species, *Uloborus diversus* and *Philoponella vicina*, seemed to be less prone to add successive radii on approximately opposite sides of the web following proto-hub removal, as occurred in aranoids (sections 6.3.3.2, O6.1.1.5.3). Alternating sides may not be feasible in uloborids, because they built hub spiral during secondary radius construction. The spider would have to had added on average approximately one hub loop every two or three radii, if new secondary radii were built on approximately alternating sides of the web; this could result in an over-sized hub (Eberhard 1990*a*).

Uloborids resembled typical araneids in laying secondary radii at “final angles” with the exit radius (Eberhard 1972). Another similarity with araneids was that, at least in *U. diversus* (Eberhard 1972), the spider strengthened or “cinched up” the longer frame lines during frame construction, sometimes quite extensively. Female *U. diversus* made up to ten trips back and forth along the newly laid frame line before returning to the hub. This species also appeared to tighten some frame lines when attaching them to the substrate, sometimes moving forward a short distance along the cage wall and then “snapping back” several times before making an attachment, just as *M. duodecimspinosa* (sections 6.3.3.1, O6.1.1.1).

O6.3.2.4 Theridiosomatids

As far as is known, secondary radius construction behavior in theridiosomatids is the same behavior as that of typical araneids, both with respect to operations and to leg movements (Eberhard 1982). These spiders are small, however, so details of leg movements have not been *observed carefully*.

O6.3.2.5 Symphytognathoid orb-weavers

Incomplete observations of species in the symphytoghnathoid families (Anapidae, Mysmenidae and Symphytognathidae) suggested that radius and frame line construction prior to sticky spiral construction was similar to that of typical araneids, including the radii built above the horizontal orb (Fig. 7.9) in anapids, and also in the entirely “3-dimensional orbs” of mysmenids (Fig. 10.21, Eberhard 1987*c*). No pattern was discerned with respect to when radii were built above the orb as opposed to those in the orb plane, except that they seemed not to be laid early in radius construction. No species built hub loops during radius construction (Table O6.2). The anapid *Anapisona simoni* built a hub immediately following secondary radius construction, but the mysmenid *Mysmena* sp. had no hub at this stage; some radii were attached to each other at a central point, but others originated on other radii near this point, and no hub loops were built (Eberhard 1987*c*).

O6.3.3 Frame lines

O6.3.3.1 Other araneids and tetragnathids

Araneid and tetragnathid frame construction was more variable, both intra-specifically and inter-specifically, than any of the subsequent stages of orb construction (see Peters 1937*a*, 1937*b*; Tilquin 1942; König 1951; Mayer 1952; Eberhard 1990*a*; Zschokke 1996). I will only describe general patterns, and not consider the variations. Construction of a new radius was generally an integral part of frame construction (e.g. Fig. 6.5e-g). But replacing a radius already in place during the trip away from the hub occurred during some frame construction sequences (Eberhard 1990*a*; Zschokke 1996). Other frames were built without any trip to the hub (Tilquin 1942 on *Zilla diodia* (= *Araneus diodius*), and still others involved laying two new radii in the process of building a single new frame line (Peters 1937*a*, 1937*b* and König 1951 on *Araneus diadematus*). The descent from the bridge line to begin lateral frame construction described for *Caerostris darwini*, which (Gregorič et al. 2011b) thought was unique to this species, may have been the lowering of the protohub to establish the definitive hub, as seen in *M. duodecimspinosa, A. diadematus* and others (Fig. 6.5d, section 6.3.3). Secondary frame lines were lacking in the orbs of *C. darwini* (Gregorič et al. 2011b).

The usual explanation for this great variability (which also characterizes frame construction in nephilids and uloborids) is that the geometric arrangement of frame lines is undoubtedly closely related to the idiosyncratic arrangements of supports for the web, in contrast with later stages of construction in which the spider oriented using the more regular and predictable array of lines that she had already laid (Witt 1965; Ades 1986). The idea that the spider gradually isolates herself from the details of her surroundings as she builds an orb is reasonable; but I am not convinced that environmental variation is sufficient to explain the substantial variations in frame construction that have been observed. For instance, *N. clavipes* performed an estimated total of 50 intra-specific variations in a uniform, geometrically simple setting (circular wire hoops) in captivity (Eberhard 1990*a*).

O6.3.3.2 *Nephila*

The extensive variation in the frame construction behavior of *N. clavipes* (Eberhard 1990*a*) differed dramatically from the behavior of *L. mariana* (TET) and *P. vicina* (UL) (Fig. O6.7). Each of the latter species showed several common patterns and a few additional rare variations; in contrast, the number of patterns in *N. clavipes* was much higher, and continued to increase even at the end of the study (Eberhard 1990*a*) (all three species were observed for approximately similar amounts of time). Most but not all of the variants in *N. clavipes* included adding two new radii along with each new frame (Figs. O6.7, O6.5), a behavior seldom that is rare or absent in most other araneoid orb weavers (except *Cyrtophora*).

O6.3.3.3 Uloborids

In *U. diversus* and P. *vicina,* legs IV reeled in slack silk during frame construction. The araneid *M. duodecimspinosa* occasionally reeled up slack frame lines during construction (Fig. 6.5d), but used her anterior legs rather than her legs IV. Some other uloborids such as *Hyptiotes* (Marples and Marples 1937; Opell 1985), *Miagrammopes* (Ackerman 1932; Lubin et al. 1978) also reeled in lines with their legs IV when holding the finished web to intercept prey.

Still another difference in frame construction by *U.* diversus and P. *vicina* was that the spider broke the newly laid frame line when she returned to the first radius laid and shifted the attachment outward along this radius before she returned to the hub (Figs. 4-8 of Eberhard 1990*a*). This may constitute a behavioral difference between uloborids and most aranoids (Coddington 1986*b*; Zschokke and Vollrath 1995b). Shifting the new frame line outward during frame construction was not unique to uloborids, however, as stated by Zschokke and Vollrath 1995b; it occurred in *Scoloderus tuberculifer* (AR) (Eberhard 1975) and *Leucauge mariana* (TET) (Fig. 14 of Eberhard 1990*a*).

One final possible difference has never been properly studied. Uloborids appear to only rarely build secondary frame lines (frame lines that span a corner formed by other frame lines). Secondary frames were "almost never" found in *U. diversus* orbs (Eberhard 1972), and a sample of 35 webs by 16 mature female *Z. geniculata* had a mean of 7.6 ± 1.6 primary frames/web but only 7 had a secondary frame (mean = 0.2 ± 0.4/web, range 0-1) (WE). Secondary frames also occurred in at least some webs of the basal uloborid genus *Waitkera* (Fig. 10.17), so it appears that if uloborids and araneoids differ, the difference is quantitative rather than qualitative.

O6.3.3.4 Theridiosomatids and symphytognathoids

To my knowledge frame line construction in these families does not differ from that in araneids and tetragnathids, though it has been little studied.

O6.3.4 Hub loops

O6.3.4.1 Other araneids and tetragnathids

There are few detailed studies of hub construction behavior. Hub construction in *L. mariana* (TET) involved the same regular, extremely rigid following movements of legs oI, oII, oIII, and oIV (Eberhard 1987*a*) as in *M. duodecimspinosa.* Leg oII grasped the radius just inside of the point held by oI, oIII grasped it just inside the point held by oII, and oIV grasped it just outside the site held by oIII (Fig. 6.12). The site (or sites) at which the hub line was attached to the radius was about midway between the points grasped by legs oIII and oIV.

A minor difference of *L. mariana* with *M. duodecimspinosa* was that leg iIII maintained its hold on the central point in the hub throughout construction of the 3-4 hub loops, rather than only during construction of the first loop. This was possible due to the smaller hub and the longer legs of *L. mariana.* The tarsus of leg iIII was ventral to the spider's cephalothorax at the start of hub construction, but by the end of hub construction the leg was nearly completely extended. It seems that leg iIII must rest at the center without seizing or otherwise becoming entangled with any lines there, because any line that was clamped by the tarsal claw would have become twisted around the claw as the spider turned; nevertheless this leg stepped away without any sign of entanglement.

The high degree of stereotypy in the leg movements of hub construction behavior probably has two important functional consequences. It helps insure that the spider advances only a single radius at a time between attachments, assuring that the hub loops form a tightly interconnected mesh with the radii, distributing stresses and perhaps also vibrations more evenly. The radius-by-radius advances insure that legs oI and oII grasp adjacent radii just after oI moves forward; in species that lay hub spiral and radii at the same time, this probably allows the spider to measure the angles between adjacent radii and to thus sense larger spaces where new radii are needed.

O6.3.4.2 *Nephila*

Hub construction in *N.* spp. formed part of the construction of most secondary radii, and radial and hub lines were continuous with each other (section O6.3.2.2). During hub construction in both *N. clavipes* and *N. pilipes* (WE), leg oI was far from the area where the lines were being added, and (in contrast with tetragnathids and uloborids), played no apparent role in guiding the spider. Instead leg oII assumed the role played by oI in typical araneids and tetragnathids, and carefully explored to find and then grasp the next radius beyond the one to which each attachment was about to be made. Leg oIII held the attachment radius at the moment of attachment, and soon afterward moved forward, following oII to grasp what would be the next attachment radius (r_n) (Fig. O6.8); iII then stepped forward immediately to find and grasp the next radius further on, while leg oIV followed leg oIII to grasp r_n. At the moment of attachment, the spider held two adjacent radii, r_{n+1} with her leg oII, and r_n with legs oIII and oIV. Presumably she sensed the separation between these radii by the positions of her legs oII and oIII at this moment, and used this information (just as typical araneids use the separation between legs oI and oII) to decide whether or not to add a radius.

Assuming that nephilids were derived from an araneoid orb weaving ancestor (Figs. 1.10, 1.15), they apparently transferred the sensory mechanisms by which they measure the distances between adjacent radii, from legs oI and oII as in typical araneids, to legs oII and oIII. Subsequently, *N. clavipes* also differed further in in using legs oI and oII rather than oI and iI to search in the sector for possible lines she might have missed, as in typical araneids and uloborids. Only late in the process, after the decision to add a new radius had apparently been made, did leg iI grasp the leading edge radius as the spider began to move away from the hub.

This reduced role of leg iI in *N. clavipes* may be related to the combination of the spider's relatively large body and the small mesh distances between lines in the hub. It may be physically difficult or impossible for the spider to manoeuver leg iI precisely so close to her body. If this speculation is correct, younger individuals of *Nephila*, which do not have such disproportionately large bodies compared with the spaces between lines (Fig. 1.5), may seize radii with leg oI during hub construction; no data are available on this point.

O6.3.4.3 Uloborids

Direct observations showed that the uloborids *Uloborus diversus* and *Philoponella vicina* (Eberhard 1972, 1990*a*) differed with typical araneids in beginning hub construction very early during radius construction. The branching patterns of radii in photographs of the hubs of finished webs (Fig. 6.11) also indicated that the hub began very early in at least six other species of *Uloborus* (Lubin 1986, WE) four of *Philoponella* (Opell 1979; Lubin 1986, WE) and *Waitkera* (Opell 1999, unpublished photos). The movments of the outer legs were strictly coordinated during hub construction in *U. diversus* and *P. vicina*, but there is uncertainty regarding the order in which they moved (IV-III-II-I?) (Eberhard 1987*a*).

The hub spiral was almost invariably attached twice to each radius it crossed, the first slightly farther from the center of the hub than the second. Double attachments of this sort, which generally resulted increased the tension on the radius (Fig. 4.9, section 4.4), were the rule in uloborids, even in the hub of the highly modified web of *Polenecia producta* (Fig. 3.44, Peters 1995). The double attachments in the hub of *Zosis geniculata* differed, however, in that they often did not pull the radius out of line (Fig. 3.46f); they were entirely absent in the outer hub loops of the resting web of a mature male (Fig. 3.48b). Double attachments were rare in araneids, tetragnathids, and theridiosomatids. They were absent, for instance, in Figures 3.5, 4.15, 3.43d, and 10.32, but they occurred infrequently in the hubs of *Cyclosa camelodes* (AR) (Shinkai and Takano 1984) and Zygiella x-notata (AR) (Figs. 39, 40 of Witt et al. 1968).

O6.3.4.4 Theridiosomatids

Careful observations showed that hub construction by *Naatlo splendida* began only after all radii had been laid (WE). In *Theridiosoma epeiroides* the hub was a single circle, not a spiral (Shinkai and Shinkai 1985), while *T. gemmosum* apparently did not build any hub loops (Coddington 1986a). Few details of leg movements were discernable. Double attachments were the rule for at least some radii in the outer loop or loops of the hub of *Epeirotypus brevipes* (TSM) (Fig. 3.8, WE), but not in those of *E. chavarria* (WE).

O6.3.5 Temporary spiral and tertiary radii

O6.3.5.1 Other araneids and tetragnathids

Tetragnathids differed from typical araneids in that their temporary spirals began abruptly, rather than gradually as the spider spiraled away from the hub (Eberhard 1982). After making the last attachment of the hub spiral, the spider moved outward along this same radius, attached her dragline again, and then continued moving in the same direction, now making temporary spiral. In *Leucauge mariana* (TET) the site where the temporary spiral began was not random. In 133 non-horizontal orbs, it tended to be in the upper rather than the lower half of the hub (85 vs 13 cases) (the other 35 initiations were at approximately the same level as the hub). When the temporary spiral began level with the hub or in the upper half, the spider was nearly always circling upward rather than downward (Eberhard 1987a).

In some other araneid species (but not M. duodecimspinosa), temporary spiral construction was often interrupted to add additional radii ("tertiary" radii of Le Guelte 1966) (Fig. 9.17). Tertiary radii were apparently common in some in araneids but not others. For instance, a mean of 1.6 tertiary radii were present in the lower half of 27 *Metepeira* sp. orbs, and they also occurred in *Z. x-notata* webs (Le Guelte 1966). But they were rare or absent in 25 *Micrathena duodecimspinosa*, 10 *Argiope argentata*, and 20 *Allocyclosa bifurca* orbs (WE). As far as is known, the sequence of attachments was typical of that in secondary radius construction (above). The new radius originated at the last attachment of the temporary spiral, and was continuous with the temporary spiral line. The details of the leg movements have not, to my knowledge been determined. Usually the spider continued to circle the web laying temporary spiral in the same direction in which she had been moving before laying the new tertiary radius

Cyrtophora and its close relatives *Mecynogea, Manogea,* and *Kapogea* were exceptional with respect to tertiary radius construction. These spiders built webs a dense, horizontal, symmetrically circular sheet with a three-dimensional tangle above and below (Fig. 1.7, Wiehle 1927; Blanke 1972; Lubin 1973; Kullmann 1975). The web lacked sticky lines. Peters (1993) showed that both the radial and spial lines in the sheet of *C. citricola* were apparently minor ampullate lines, on the basis of their diameters. The radii spilt repeatedly into numerous tertiary radii, so there were many more radii near the outer edge of the sheet than near the hub. The spiral may be homologous with the hub rather than the temporary spiral. One detail of *C. citricola* sheet construction that supported the hub homology hypothesis was that leg iIV did not grasp the current segment of temporary spiral (WE), and the tensions on these spiral lines were thus presumably no greater then the force necessary to pull the lines from the spider's spinnerets. In contrast, *M. duodecimspinosa,* iIVconsistently held the dragline at the moment the attachment was made during temporary spiral construction (section O6.2.4). The lines were so short during *Cyrtophora* sheet construction, and the attachments were so rapid (on the order of 4/s in *C. citricola*) that it may be difficult for the spider to regrasp her dragline with leg IV.

The sheets of *Cyrtophora* webs had astronomical numbers of attachments. For example, in one especially clear photo of a nearly complete sheet of *C. citricola* (Fig. 83 of Kullmann 1975), there were 99 loops of spiral. In a 39^o sector of this web, there were 30 radii at the outer edge, 30 radii three quarters of the distance from the center of the hub to the edge, 26 half way out, and 16 a quarter of the way out.

Estimating the numbers of radii at different distances by interpolation gives approximately 2352 radius-spiral junctions in this sector, or about 21,700 for the entire (still incomplete) sheet!

A dense web design like this is only feasible because of the extraordinary speed and precision with which these spiders worked while they built their sheets. Kullmann (1958) measured the rate of attachment as 3.7/s, while one intermediate-sized female nymph of *C. citricola* that was filmed while she was perhaps half way through sheet construction on a warm morning made about 4.2 attachments/s (WE). This speed is almost unbelieveable when one takes into account that each of the four outside legs was moved in a very precise way prior to each attachment: each leg advanced one radius, with leg oII following leg oI, and leg oIII following leg oII. And the legs were not simply finding and grasping new lines with each movement – they were also measuring distances (witness the highly regular spacing between the spiral lines – Fig. 1.7). Even small details of the spider's behavior were precise: her leg oI searched for each new radius with a medially directed swing that brought its prolateral surface into contact with the line; the length of time that the spinnerets made contact with the radius appeared to be, at least in some cases, only 0.03s (the limit of resolution of the 30 fps video), so initiation and termination of the piriform lines and glue was probably even shorter. The tension on the spiral was also relatively constant, because each attachment to a radius pulled the radius into zig-zag configurations with relatively consistent angles (Fig. 1.7).

O6.3.5.2 *Nephila*

Several details of temporary spiral construction in nephilids differed from that of *M. duodecimspinosa*. Temporary spiral construction has only been described in detail in *Nephila pilipes* (= *maculata*) (Hingston 1922b) and *N. clavipes* (Eberhard 1982, WE), but details of the positions of lines and their attachments in the finished webs of the other nephilid genera in which the temporary spiral also remains intact suggest that their behavior may be similar. The temporary spiral was a continuation of the hub spiral; the spaces between loops increased gradually as the spider began to move away from the hub, and then remained at least approximately constant in the rest of the web. Spacing was reduced near the points where the spider reversed direction. The temporary spiral of *Nephila* spp. differed from that of *M. duodecimspinosa* in being attached twice to each radius that it crossed, with the first attachment slightly farther from the hub than the second (Fig. 4.4). I was only able to perceive a single dab of the abdomen as it was built, so her spinnerets presumably just slid a short distance inward along the radius to make the second attachment.

The spider faced inward toward the hub while laying the temporary spiral, and moved sideways across the web; her anterior end was several loops inward of the site where she was laying the new temporary spiral. Leg movements suggested that leg oI may give the spider information on the location of the outer loop of temporary spiral already in place, and thus guide the choice of attachment sites. Leg oIII, which was used to guide hub construction (section O6.1.1.5.4), did not consistently contact the outer loop, nor did oIII. Leg oI, in contrast, consistently tapped in the area several radii ahead of the current attachment radius and then slapped medially to hit and grasp the outer loop. The leg moved only about once every 3-4 attachments, however, so it could provide general information on the location of the outer loop, not for the precise site where it intersected the radius to which the temporary spiral was about to be attached. This general level of guidance is probably similar to that which *N. clavipes* may derive from leg oII during sticky spiral construction (section O6.3.6.3).

The hypothesis that oI is used as a guide was supported on three occasions when leg oI made several "mistakes" in a row. It grasped the penultimate rather than the outmost loop of temporary spiral during 3-5 consecutive steps, and in all three occasions the path of the new loop of the temporary spiral loop that the spider was building veered inward gradually. The response was, however, slow and far from complete, so there may also be some sort of behavioral "inertia" (perhaps from memories of previous attachments - section 7.4.1).

Some turnbacks in the temporary spiral were preceded by movements of the oI to grasp the penultimate rather than the outer loop, so swinging oI farther toward the hub than normal may be a preliminary to turning back. The turnback itself involved little reorientation of the spider's body; if she had been moving toward her left side, she simply began moving toward her right, or *vice versa*. The spaces between temporary spiral loops were usually reduced for 1-2 radii following a turnback, and were occasionally reduced to 0, with the new loop was laid on top of the previous one. Similar reductions in spacing have also been seen in the araneid *Zygiella x-notata* (Le Guelte 1966) and the uloborid *U. diversus* (Eberhard 1969, 1972).

Tertiary radii were common, and were built during temporary spiral construction, as in araneids. T hey were built in pairs, as in secondary radius construction. The consistent sequence of the positions and movements of the spider's legs during temporary spiral construction suggested that the spider sensed the size of the sector between adjacent radii, which presumably guided her decision regarding whether or not to add tertiary radii, using her legs oII and oIII, again as in secondary radius construction. Leg oIII consistently held the attachment radius, and oII held the radius just beyond at the moment of attachment of the temporary spiral (as in hub construction – see above). The spider always used the upper of the two radii bordering the sector as the exit radius. When she finished a new pair of radii and resumed temporary spiral construction, the spider generally (always?) continued in the same direction that she had been moving just before (as in hub construction). In some cases, when *N. clavipes* built the next loop of temporary spiral, she fastened a newly built tertiary radius to its neighbor, leaving a pattern in the finished web in which the tertiary radius appeared to originate on this neighboring radius. Behavior of this sort may have been responsible for one type of tertiary radius construction observed in *N. clavata* by Shinkai (1985).

O6.3.5.3 Uloborids

The transition from hub to temporary spiral was gradual rather than abrupt in several uloborids (Eberhard 1982; Lubin 1986). In *Uloborus diversus*, the spider did shift more or less abruptly, however, from making double hub spiral attachments to each radius to making single attachments of the temporary spiral. Occasionally, in *U.* sp. "MB" (Lubin 1986), Fig. 3.31 of *U.* sp., Fig. 6.11 of *U. diversus*, photographs showed a brief shift from single back to a short series of double attachments near the outer edge of the hub. In *U. barbipes*

(Lubin 1986) and the web of a mature male *Z. geniculata* (WE) the transition from double to single was earlier, so that the inner loops of the hub had double attachments, but the outer loop attachments were single (Lubin 1986).

Very occasionally the temporary spiral of *U. diversus* was attached twice to a radius; in such cases the temporary spiral and pulled the radius out of line (plate X in Eberhard 1972), showing that the temporary spiral was under appreciable tension.

The only detailed behavioral observations are of *U. diversus* (Eberhard 1972). This species differed in several ways from typical araneids. In contrast with *A. diadematus*, the spider did not always turn to face toward the hub each time she attached the temporary spiral to a radius; near the edge of the web faced as much as 60° away from the hub. The distance between the loops of temporary spiral increased in the first loops until it reached about one body length, and then remained more or less constant. Sometimes, however, the distance between loops decreased very sharply near the outer edge of the web when the temporary spiral was close to a frame line; in extreme cases, one loop was laid directly on top of another (Plates IV and X in Eberhard 1972). This level of reduction in temporary spiral spacing has never to my knowledge been seen in any other family of orb weavers, though smaller reductions may occur near frames in *M. duodecimspinosa* (Fig. 6.10) (systematic measurements are lacking).

There were several similarities between *U. diversus* and araneids. Legs oIII and oIV gripped the radius, and iIV held the dragline (i.e., the new segment of temporary spiral) at the moment of attachment. Only seldom (near the outer edge of the web) did the temporary spiral cross a radius without making an attachment. Photographs of webs with intact temporary spiral lines showed that many temporary spiral turnbacks occurred in the vicinity of frame lines, but more than a body length away. Thus spiders probably often turned back without having actually touched the frame; direct observations showed that spiders did not move beyond turnback points (see also *Nephila* above, and section 6.3.4). When executing a turnback, the spider turned to face “inward”, toward the hub as she made the turn.

Spiders sometimes added tertiary radii during temporary spiral construction. Some tertiary radii originated at a temporary spiral–radius junction, while others were attached to an intact temporary spiral line. Tertiary radii were typically bent away from the nearest radius by subsequent loops of temporary spiral (Eberhard 1972), as also occurred in araneids such as *Z. x-notata* (Le Guelte 1966) and *Nephila* spp. (section 4.3.3.2). The details of tertiary radius construction operations and the leg movements varied too much in *U. diversus* (Eberhard 1972) to allow simple comparisons with araneids and nephilids. Tertiary radii were infrequent in the *U. diversus* (0.2 per orb in 21 webs) and *Zosis geniculata* (0 in 23 orbs) (WE).

One detail of temporary spiral construction apparently changed during ontogeny in *Uloborus diversus*. The relative spaces between loops were smaller in second instar nymphs, in relation to the size of the spider’s body, than in older spiders (Eberhard 1975), but this difference was not quantified. A tighter temporary spiral mesh may be mechanically advantageous in these webs, which lacked sticky spiral lines, and in which there were no other lines binding radii together.

O6.3.5.4 Theridiosomatids and symphytognathoids

The temporary spiral was modified in the families of tiny orb weavers. It consisted of one or several concentric circular lines in Theridosomatidae (Eberhard 1972; Shinkai and Shinkai 1985; Coddington 1986*a*), and was entirely absent (perhaps convergently) in at least some species of in the symphytognathoid families Anapidae and Mysmenidae (Eberhard 1972, Lopardo et al. 2011). Construction behavior in theridiosomatids differed from *M. duodecimspinosa* and other araneids in that the spider lost contact with the outer loop of temporary spiral (or with the hub, while making the first loop) as she moved outward along each radius to make an attachment. The likely cue guiding the placement of these attachments is a kinesthetic sense (section 7.4.1). The functional significance of a circular rather than a spiral pattern of the temporary spiral is uncertain.

The function of the omission of the temporary spiral in anapids and mysmenids may be that it facilitates extension of the sticky spiral to radial lines above the plane of the orb. If a spider laying sticky spiral while walking under the radii in a typical orb with temporary spiral lines attempted to climb up radial line above the web plane, her sticky line would be unable to get above the orb’s plane due to the temporary spiral lines (Eberhard 1987*c*) (see, however, the discussion of *Maymena* sticky spiral construction below).

Perhaps as a result of the reductions in temporary spirals, tertiary radii were apparently completely absent in the orbs of species in the families of tiny orb weavers (Table O6.2). Supplementary radii were laid following sticky spiral construction in at least three species, and they probably had the same function of filling in spaces between radii in the outer portion of the orb (see below).

O6.3.6 Sticky spiral

O6.3.6.1 Other araneids

Leg and body movements during sticky spiral construction were more or less consistent in other araneids: the spider started at the outer edge of the web and worked inward. Following behavior was frequent during sticky spiral construction (Table O2.2). Details of consistent movements of Alpaida rhodomelas (Fig. O6.1) included the following.

Leg oI: was in the air near rn-1 while the attachment was made (0-0.67). It moved variably as the spider walked inward along rn-1 and along the temporary spiral (1.11-1.56). It grasped r_n, followed by leg oII (1.56), and then extended laterally parallel to r_n and tapped several repeatedly until it touched the inner loop of sticky spiral (4.89). It then immediately stopped tapping, and the spider began to turn to attach (5.11- 5.56).

Leg oII: made irregular movements immediately after the attachment to r_{n-1}, then followed leg oI to grasp and move outward along r_n in using a "hand-over-hand" motions in coodination with oIII (various stages illustrated in 1.78-2.89). Immediatly after leg oI touched the inner loop (4.89), oII ceased the hand-over-hand movements and swung anteriorly while the spider turned to attach.

Leg *oIII*: moved irregularly until it began reeling in r_n "hand-over-hand" with oII. It maintained its grip on r_n after oI contacted the inner loop (4.89) as the spider turned to attach.

Leg oIV: held r_{n-1} just beyond the attachment point while the attachment was made (0), moved along r_n (0.67, 1.11), and began to pull out sticky spiral line (e.g., 1.78, 2.00) as the spider moved toward r_n, at first by itself and later, near the attachment site on r_n, in alternation with iIV (e.g. 4.44, 4.89). As the spider turned to attach, oIV seized rn just beyond the point where oII held it (5.56), and these two legs held rn against her spinnerets as the attachment was made (as seen in 0).

Leg iIV: pulled out the sticky spiral line just as it was attached to r_{n-1} (0), and then helped support the spider as she moved inward along r_{n-1} and along the temporary spiral (1.11-1.78). Then it pulled out sticky spiral line (e.g., 2.89-4.44), at first alternating with oIV and later making consecutive pulls by itself; the last pull occurred (5.56) as the new line was attached to rn (from Eberhard 1982 - traced from movies).

Perhaps the best documented difference between other araneids and *M. duodecimspinosa* was that in nearly all araneids (as in *A. diadematus*) leg oI was used to find the inner loop instead of oIV (Fig. O6.1 frames 80, 88), while tetragnathids used leg iI to find the inner loop (Fig. O6.2) (Eberhard 1982).

One detail of sticky spiral construction behavior that clearly varied both inter- and intra-specifically, and which undoubtedly had important consequence for the orb's ability to capture prey, was the spider's use of her legs IV to pull out additional sticky line. All araneoid orb weavers, as far as I know, lengthened the sticky line just before they attach it to each radius by pushing on it with leg iIV just before the attachment is made (time 0 in Fig. O6.1; time 1.67 in Fig. O6.2, 1.06 in Fig. O6.3) (Eberhard 1982). In some species like *M. duodecimspinosa*, this was the only contact with the new sticky line until leg iIV pulled out additional line again just before the next attachment; but in many other araneids, like *A. acuta* (= *rhodomelas*), *Araneus expletus*, and *Gasteracantha cancriformis* (AR), additional silk was also pulled out with repeated, posterior-ventrally directed movements of one or both legs IV while the spider moved from one attachment to the next (times 4.44 and 4.89 in Fig. O6.1. The araneid *Allocyclosa bifurca* differed in that she did not pull additional line until she had reached the attachment site, and then made only a few pulls before attaching (typically three, all with leg iIV) (WE). A mature female *G. cancriformis* averaged 12.9 ± 1.5 pulls/segment near the outer edge of an orb, but only 3.9 ± 1.2 pulls/segment near the inner edge of the capture zone, while an *A. expletus* female averaged about 8 pulls between each pair of attachments of the sticky spiral in the outer third of her orb (counting the final pull just before the attachment) (WE).

The pulls lengthened the segment of sticky line and thus lowered its tension. Lower tensions will increase its ability to stop and to retain prey (sections 3.3.3.1, 4.4); presumably additional pulls were needed because the tension needed to draw the highly extensible line from the spinnerets would have otherwise resulted in the line being under higher tension and thus in a more extended state in the finished orb. A lower tension will also, however, increase the segment's susceptibility to wind damage (section 3.2.11.3.2), and also raise the cost of the sticky spiral in terms of material investment. The differences between the numbers of pulling movements of different species may thus represent adjustments with important consequences for orb function.

Video recordings revealed that *Argiope argentata* (G. Barrantes unpub.) and *A. trifasciata* (WE) used leg oI somewhat differently during inner loop localization behavior. Instead of tapping toward the inner loop where it crossed r_n (the radius to which she was about to attach her sticky line), as in other araneids, leg oI consistently touched the inner loop near the next radius, just beyond the attachment radius (e.g., near r_{n+2} rather than r_{n+1} in Fig. 6.15). Most likely this contact served as a general guide to the location of the inner loop. It appeared that the precise site for the attachment was influenced by leg oIV, as in *M. duodecimspinosa*. In both *Argiope* species leg oIV followed leg oIII to grasp r_n, and then usually slid outward along r_n until contacting the inner loop; it usually grasped the radius at the junction with the inner loop. Occasionally oIV sometimes stopped short of the inner loop, however, and grasped the radius inside of this junction, as in *M. duodecimspinosa* (Fig. 6.27); thus the spider my have remembered the location of the site touched by oI when she attached to r_{n+2}.

A second behavioral variation occurred in the outer portions of the orbs of moderately short-legged species such as *A. acuta* (AR) (Fig. O6.1) and *Gasteracantha cancriformis* (AR) (WE). Instead of walking along the radius to reach the inner loop of sticky spiral, the spider held onto the temporary spiral and reeled in the attachment radius (r_n) hand-over-hand with legs oI and oII; the portion of the radius between the temporary spiral and where the spider gripped it with her leg oII or oIII became slack. In effect, this behavior allowed the spider to attach loops of sticky line farther from the outer loop of temporary spiral without losing contact with the temporary spiral, and thus "compensated" for making a less extensive temporary spiral. Reeling in the radius would thus result in a small savings in the amount of silk invested in the temporary spiral, though it is not clear whether the amount saved would be biologically significant in light of the probable additional energy needed to reel in the radius rather than simply walking along it. A more likely hypothesis is that reeling in the radius reduced the distortion of the web produced by the spider's own weight, especially in the local area where the attachment was to be made (Fig. 6.24), and may thus have made it more feasible for the spider to lay lines with lengths and spacing between them that were appropriate for the finished web. Tetragnathids and uloborids, in contrast, apparently always walk along r_n rather than reeling it in. This preliminary association between reeling in and having relatively short legs is in accord with this hypothesis. Reeling in the radius rather than walking along it may be a useful taxonomic trait, but its detailed distribution is not known.

The use of the temporary spiral lines as bridges between radii for multiple loops of sticky line was reflected in the "bundling" of the tracks of spiders building the sticky spiral (Fig. 6.25). Zschokke & Vollrath (1995a,b) suggest that bundling did not occur in a uloborid, but grouping of lines was nevertheless discernible in *U. walckenaerius* (Fig. 6.25), especially in the outer portion of the web where radii were farther apart and the spider needed the temporary spiral bridges to move from one radius to the next. Direct observations of other uloborids (*Uloborus diversus* and *Zosis geniculata*) confirmed that these spiders also moved inward to repeatedly use the same temporary spiral lines as bridges between radii while they were laying the sticky spiral in the outer portions of their orbs (Eberhard 1972, WE).

In some larger, slower-moving species it could be seen that there was some variation in point on leg oI that contacted the sticky line (Eberhard 1982). This variation is in accord with the idea that the spider relied on tactile cues, and was thus uncertain of exactly where she would encounter the line (section 7.1.1).

O6.3.6.2 Tetragnathids

Inner loop localization behavior in tetragnathids differed consistently from that in araneids (Eberhard 1982). As the spider moved outward along r_n toward the inner loop of sticky spiral, she turned to face more or less parallel to the radius (r_n) and walked forward, rather than moving laterally like araneids. She used her leg iI rather than oI to locate the inner loop (Fig. O6.2 frames 17 - 21), extending it anteriorly toward the inner loop with its tip bent ventrally (upward in species with horizontal orbs), with its tip more or less in the plane of the orb. This apparent searching movement ended the moment the dorsal surface of tarsus iI touched the inner loop (in contrast, contact was with the ventral surface in araneids). The spider immediately turned her body toward the hub, and began the process of attaching the sticky line (Eberhard 1982). Similarities with typical araneids included the following: the tapping and other outwardly directed movements ceased immediately after leg iI contacted the inner loop (1.11 in Fig. O6.2) and the spider immediately turned to attach; leg oIII followed leg oII on r_n (1.22), and leg oIV followed leg oIII on r_n (1.33); and legs oIII and oIV held r_n against the spinnerets and leg iIV pulled sticky spiral line as the attachment was made (1.67). Following behavior also occurred frequently during sticky spiral construction (*Leucauge mariana* in Table O6.2).

O6.3.6.3 Nephilids

Inner loop localization behavior using leg oIV in nephilids (reviewed by Kuntner et al. 2008a) resembled the most common behavior of *M. duodecimspinosa.* Differences with typical araneids included the following (Fig. O6.3). The spider faced inward (toward the hub) the entire time; none of her legs I or II touched lines near the attachment site, and they changed grips much less often than attachments were made; leg oIII did not follow leg oII, and tapped or waved to find r_n following each attachment; and leg oIV slid outward along r_n to contact the inner loop (in smaller, immature individuals, leg oII was directed retro-laterally and tapped toward the inner loop of sticky spiral and usually touched it before most but not all attachments; contact with the inner loop was made several radii in advance of the radius where the attachment was about to be made). Similarities with typical araneids included the following: leg oIV followed oIII to rn; and legs oIV and oIII held r_n and pressed it against the spinnerets at the moment of attachment, and at the same time leg iIV pulled additional sticky line from the spinnerets.

The use of leg IV for inner loop localization was confirmed in *N. pilipes* (= *maculata*) by experimental alterations of the web, and by removing the tip of the leg (Hingston 1922b). The convergence with *M. duodecimspinosa* was associated in both groups with the relatively large size of the spider's body compared with the distances between lines in the orb. Use of leg IV allowed the spider to step more nearly laterally, directly from radius to radius, and thus reduced reorientation movements of her body between successive sticky spiral attachments. Hingston (1922b) noted that leg oIV maintained its hold on the radous immediately following the attachment, and pushed against the radius while the spider's abdomen was pulling away from it, thus drawing the first portion of the next segment of sticky spiral from her spinnerets.

The relatively large pair of sub-esophageal ganglia associated with legs IV in *N. clavipes* (R. Quesada et al. unpub.) may be associated with the use of legs IV to locate lines in orb construction (a possibly related difference is that these spiders sometimes return to the hub "backward" after attacking prey, climbing the drag line "hand over hand" with their legs IV – Robinson and Robinson 1973*a*). Comparisons of details of the tracts in this ganglion between *Nephila* and more typical araneids or tetragnathids could help clarify the as yet nearly completely unknown functional significance of different details of orb weaver brains (Table O10.1).

In *N. pilipes* leg oIII followed oII, and leg oIV followed oIII (Hingston 1922b), and oIV also followed oIII in *N. clavipes* (WE). These species thus differed from *M. duodecimspinosa* in lacking following behavior in some legs, such as oII following oI. These legs of *Nephila* are relatively long, and they grasped lines relatively far from the attachment site and moved less frequently than attachments were made.

Details of additional movements of appendages during sticky spiral production have been described in *N. pilipes* (Hingston 1922b) and *N. clavipes*. The anterior lateral spinnerets of *N. clavipes* rapidly rubbed their distal surfaces against each other at the moment of attachment. These movements were precisely coordinated with the movements of the abdomen and legs oIII and oIV that held the radius briefly (for about 0.03-0.1s) in the groove between the bases of the AL spinnerets. Similar spinneret movements probably also occur in other araneoid orb weavers, whose smaller sizes and more rapid movements make them difficult to observe. Nephilids resembled tetragnathids and uloborids, and contrasted with some araneids in that they never, to my knowledge, reeled in radii during sticky spiral construction.

O6.3.6.4 Uloborids

O6.3.6.4.1 Inner loop localization

The inner loop localization behavior of uloborids resembled that of araneids, and differed from that of tetragnathids and nephilids, in that the spider used her laterally extended leg oI to tap repeatedly toward the inner loop of sticky spiral as she sidled outward along the radius (Eberhard 1982). As in araneids, the spider usually immediately ceased tapping as soon as her leg oI contacted the inner loop, and turned to grasp r_n with legs oIII and oIV preparatory to making an attachment. In *Zosis geniculata* (UL) leg oIV swung forward to contact r_n near oIII, and then slid outward along this radius before grasping it during this turn. This sliding movement resembled that of leg oIV of *M. duodecimspinosa* (AR) and *N. clavipes* (NE), but differed in that oIV always stopped far short of contact with the inner loop of sticky spiral; thus it probably did not function in inner loop localization. In *Z. geniculata* the spinnerets contacted the radius nearly exactly half way between oIII and oIV. The spider always walked outward along the radius, rather than reeling it in, as in some araneids.

The rapid combing movements of legs IV used by uloborids to pull the cribellum fibrils from the cribellum differed from all araneoids. These movements showed several consistent patterns. In *Uloborus diversus* (UL) (Eberhard 1972) and *Z. geniculata* (WE), the spider always began combing with leg oIV after attaching the sticky line to a radius; and then always shifted to combing with iIV before reaching the next radius (oIV grasped r_n to hold it against her spinnerets for the next attachment). In *Z. geniculata*, initiation of combing usually occurred after the spider had pulled slightly away from the attachment, often leaving a short segment of the spiral in which the cribellum lines were tight rather than piled up loosely, and less sticky (many such small spaces are visible in Figs. 7.1 and 7.19; they betrayed the direction in which the spider had been moving while she laid the sticky spiral). In *Sybota* sp., these spaces were relatively large (on the order of a tenth the length of the segment) (Grismado 2001). She combed continually as she moved to reach the next radius, and then continued to comb for up to a second or more before attaching. Simultaneously with each rearward combing movement of leg IV, the long posterior lateral spinnerets of *U. walckenaerius* (Peters 1984) and *Z. geniculata* (WE) moved posteriorly briefly. Peters (1984) proposed that these spinneret movements packed the mat of cribellum fibers around the sticky spiral baseline; higher magnification observations will be needed to confirm this and describe how packing occurs.

A second unusual pattern of uloborid sticky spiral lines was the zig-zag pattern of sticky spiral in the outer loops (including the genera *Waitkera, Conifaber, Uloborus, Philoponella, Zosis* and, at least occasionally, *Waitkera*) (Eberhard 1972, Lubin et al. 1982, Lubin 1986, Opell 1999, unpub. photographs of *Waitkera*, Grismado 2008, Eberhard and Barrantes 2015) (*Sybota atlantica* may be an exception – Grismado 2001). The spider made two successive attachments to the same radius before going on to the next radius (Fig. 7.24). In one *P. undulata* web, zig-zag attachments occurred all the way to the inner loops of the sticky spiral (Lubin 1986). In all cases in which the direction of the spider's movement could be determined (direct observations of *U. diversus*, tracing the spider's path in *U. trilineatus* and *Z. geniculata*), the spider moved inward rather than outward along the radius to make the second attatchment. Zig-zag sticky spiral attachments resembled the sticky line production in the derived webs of *Polenecia producta* (UL) *Miagrammopes* spp. (UL), in which the spider attached sticky lines repeatedly to each radius or to a single line while moving toward the hub or resting site (Peters 1995, Lubin et al. 1978). Zig-zag sticky spiral attachments are nearly unknown in other orb weaving spiders. They only occur, to my knowledge, in the intermediate forms of the highly modified "sawtooth" orb of *Eustala* sp. (Fig. 7.25), where they were also produced while the spider moved inward rather than away from the hub. Placing sticky silk on a radius would make the compound sticky line more difficult to break, but increase the spacing between sticky lines. Possible functions for zig-zag sticky lines include to increase the trapping surface (Lubin 1986), or to modify the outer portion of the orb to capture larger prey (WE).

O6.3.6.4.2 To attach or not to attach: skipping radii

Photos of the orbs of many uloborids, including species in the genera *Uloborus, Philoponella, Zosis, Waitkera* (Wiehle 1927, 1929, 1931, Peters 1954, 1984, Eberhard 1972, Lubin 1986, and Opell 1979, 1999, unpub. photographs) show that uloborid sticky spiral lines were not always attached to each radius that they crossed, especially in the inner portion of the capture zone. On the other hand, I know of no other orb weavers that skip radii; either skipping is a synapomorphy of deinopoid orb weavers (subsequently lost in deinopids) or, attaching to all radii is a synapomorphy of araneoids.

Neither the function of skipping radii nor the stimuli that are used by spiders to guide the decision of whether or not to skip a radius are not clear. Skipping radii economized on energy and material costs, as the spider reduced the distance that she needed to move during sticky spiral construction and the length of sticky line (and thus the number of possibly expensive combing movements with legs IV; see section 10.8.2), and the amount of piriform silk for attachments. Another consequence of skipping radii is that the spaces between loops were increased, but this could have been accomplished without skipping, simply by changing the distances between loops. The sticky spiral was more easily pulled away from the radii to which it was not attached (WE); this could increase the extensibility of this otherwise relatively rigid line (Lubin 1986).

With respect to cues triggering the decision whether or not to skip a radius, they could be as simple as an indicator of the length of the current sticky spiral segment such as the distance walked, the time elapsed, or the number of combing movements since the previous attachment. In a simulation study use of a length criterion ("attach to the current radius if the length of the current segment is above a threshold value; go on to the next radius if not"), resulted obtained patterns that were at least superficially similar to those in normal orbs of *U. diversus* (but the similarity was not tested quantitatively). Webs of *Zosis geniculata* orbs built in very small containers (Fig. 7.42; Eberhard and Barrantes 2015) suggested that a simple length criterion is too simple, however. These spiders attached the sticky spiral to each radius, even in the innermost portions of the capture zone where the distances between radii were relatively small. By attaching to each radius, the spider took better advantage of the unnaturally small space available by not leaving the larger spaces between the sticky lines that would have resulted is she had skipped radii (see Fig. 7.38b).

O6.3.6.4.3 Sticky lines on and beyond frame lines

Some uloborids such as *Uloborus diversus* (Eberhard 1972), *U.* sp. J (Lubin 1986), (Opell unpub. photos) and (to a lesser extent) *Zosis geniculata* (WE) seemed especially prone to attaching the sticky line to frame lines (Fig. 7.24). Perhaps associated with this trait, some segments of sticky lines were laid just outside the frame lines. My impression is that araneids and tetragnathids only very occasionally attach one or a few segments of sticky spiral to a frame line, and Lubin 1986 reported a similar impression and generalized that uloborids show greater frequencies of attaching sticky spiral to various types of non-sticky lines, including radii, frames, barrier webs, and egg sac webs. Sticky spiral lines beyond the frame lines were more common in both *Zosis genicula* and *Leucauge argyra* (TET) when spiders were confined in abnormally small spaces (Eberhard and Barrantes 2015). The tendency to build in constrained websites in the field in *U. diversus* and several other *Uloborus* species, as well as *P. tingena* and *Lubinella morobensis* (Eberhard 1973; Lubin 1986) may explain why sticky lines are placed on and beyond the frame lines. The uloborid willingness to attach sticky lines to frames may be associated with a second possible, but as yet even less well-documented uloborid pattern – to circle the entire web with the first or second loop of sticky spiral line, even when the orb is highly asymmetric (WE).

O6.3.6.4.4 Other details

The details of how and where temporary spiral lines are broken during sticky spiral construction have never been studied. At least some uloborids seem to be less consistent in breaking the temporary spiral (see Fig. 7.24) than are araneids and tetragnathids. For instance, 9% of an estimated 4111 segments of temporary spiral in 27 webs of *Zosis geniculata* were intact (WE). In webs of *M. duodecimspinosa* that were unpowdered (and in which sticky and non-sticky spiral lines could thus be distinguished confidently), the corresponding number was 7% of 2553 segments (see Fig. 7.26). On the other hand, intact temporary spiral segments were much less common in many other species. In 26 orbs or *Leucauge mariana* (TET), for instance, there were only two intact segments of temporary spiral; this corresponds to only about 0.1% of 1818 segments intact, on the conservative assumption of three temporary spiral loops/web.

In addition, the sites of the unbroken lines in uloborid webs were often far from the hub. In *Z. geniculata* webs, intact segments were common in the third loops (20.7%), and the fourth loop or farther outward (25.5%). In contrast, nearly all (92.9%) of the intact segments in *M. duodecimspinosa* webs were in the inner two loops of temporary spiral, as was also the case for both of the intact segments in *L. mariana.*

These figures are only estimates. The numbers of unbroken segments may be slight underestimates, because an intact segment of temporary spiral with a sticky spiral line on top of it would have been counted as broken. In addition, the total counts of were based on the numbers of radii and mean number of loops of temporary spiral. But the magnitudes of these differences suggest real differences; further counts will be needed in other species to quantify this difference more fully.

During construction of the first loop of sticky spiral, uloborids sometimes moved beyond the outer loop of tsp and lost contact with it, or (less commonly) even beyond the frame line (e.g. Fig. 3.26); in other webs, however, they remained in contact with the outer loop, as was usual in araneids and tetragnathids (Eberhard 1982).

O6.3.6.5 Theridiosomatids and symphytognathoids

Sticky spiral construction behavior resembled that of tetragnathids, in that the spider faced outward as it moved away from the temporary spiral, and used leg iI to locate the inner loop (this detail was slightly less certain, because the small body sizes and brisk movements made direct observations more difficult). But there were two common differences. In the inner as well as in the outer portions of the orb the spider often lost all contact with the temporary spiral as she moved outward to make an attachment (e.g., Shinkai and Shinkai 1985). In addition, in some (and perhaps many) the spider often stopped short and attached without touching the inner loop of sticky spiral. These spiders thus often made decisions regarding where to attach their sticky spiral lines without direct cues from lines in either the temporary spiral or the sticky spiral. This lack of use of the inner loop as a guide was especially dramatic on the radii extending above the plane of the web in some anapids (Fig. 7.9) and the mysmenid *Mysmena* sp. (Fig. 10.21). These radii often had only a few, widely spaced sticky lines attached to them (spaces were usually much larger than the length of the spider’s body). Despite the general lack of temporary spiral or sticky lines to use as a guide, the distance from the hub along these up radii at which the spider attaches the sticky loop is similar to those where it had been attaching to radii in the plane of the orb just previously. It thus appears that these groups use only kinesthetic cues to guide the placement of sticky spiral attachments, rather than a mix of kinesthetic and tactile stimuli as in typical araneids and tetragnathids (see Chapt. 5).

At the level of leg movements, at least one theridiosomatid (*Naatlo splendida*) used one leg III to reduce the danger of sticky spiral lines adhering to others during construction. When she walked inward toward the temporary spiral just after attaching the sticky line, she held the radius away from her body with one leg III extended ventrally. It was held relatively immobile (it did not take steps), and the radius apparently slid through the tarsal claw (Fig. 6.26). The function of this behavior was probably to reduce the danger that the sticky line would touch the radius and adhere to it (Eberhard 1981*a*). This precaution was particularly appropriate in the outer loops of this species, because the temporary spiral consisted of only two circles, and the outer loops of sticky spiral were far from these temporary spiral lines. A similar precaution would also be appropriate in symphytognathoids, where the temporary spiral was omitted completely and the spider’s inward trips during sticky spiral construction were even longer. Further observations will be needed to check whether leg III is used the same way in these groups.

Two further differences occurred in construction of the 3-D orbs of the tiny *Mysmena* sp. The spider pulled repeatedly with her legs IV on the sticky spiral line just before attaching it to a radius, thus causing it to become very slack and hang in a caternary in the web (Fig. 10.21). In addition, she apparently slid one leg along the radius as it moved outward to attach the sticky spiral. This behavior was not seen directly (mature females are only about 0.5 mm long!), but deduced from observing that when the radius was coated with tiny water droplets, this water was cleaned off the radius where the spider had moved, and a droplet accumulated just short of the point where the sticky line was attached; it was not determined which leg was involved.

One mystery that is yet to be solved occurs during sticky spiral construction in *Maymena* sp. (MYS). As in anapids, the sticky lines attached to the radii above the plane of the approximately horizontal orb of this species were continuous with the sticky spiral in the orb, and were built as part of sticky spiral construction. In contrast with the anapids, however, these spiders build a temporary spiral. Thus it was not clear how, when the spider attached the sticky line to a radius above the orb, walks to the hub, and then climbs up these radii (Eberhard 1987*c*), the sticky line remained above the plane of the orb (and thus above the temporary spiral) during the trip up the radius.

O6.3.7 Hub modification

O6.3.7.1 Other araneids

Most araneids differed from *M. duodecimspinosa* in that they immediately fill the hole produced when they removed the center of the hub following completion of the sticky spiral. The spider attached her dragline repeatedly to the inner portion of the remaining hub as she turned while removing the center of the hub; the new lines spanned the hole she had just produced. In *Argiope argentata* (AR) replacing the former lines with new lines resulted in complex changes in the tensions on radii in different sectors of the orb, with some increases and some decreases (Eberhard 1981*a*) (Fig. 4.17). *Caerostris darwini* did not remove the center of the hub (Gregorič et al. 2011b). Filling the hub hole has never been studied carefully.

O6.3.7.2 Other families

Hub removal is omitted entirely in nephilids and uloborids. These groups also differed from others in not performing break and reel behavior during radius construction, and thus in lacking accumulations of loose fluff in the central area of the hub. This correlation supports (though with a small sample) the “clean up” hypothesis for the function of hub removal following sticky spiral construction (section 4.9.2).

Species in Theridiosomatidae and the symphytognathoid families differed sharply from other orb weavers in how they modified their orbs following the completion of the sticky spiral. In *Anapisona simoni* and *Anapis keyserlingi* (AN), *Patu* sp. (SYM), and *Mysmena* sp. and *Maymena* sp. (MYS), the spider loosened most of the radii (sometimes all) after finishing the sticky spiral, one by one. She moved outward on the radius a short distance (less than the distance to the inner loop of stsp), broke the radius, turned 180° and attached the outer broken end to her trail line, and reeled up the other end as she moved back to the hub. She released more trail line than she reeled up, and thus lowered the tension on each radius. At least some of the radii above the plane of the horizontal orb were also loosened in this way in *A. simoni*. In *Mysmena* sp. and *Maymena* sp. the spider lowered the tension by pulling additional line with her legs IV just before attaching the radius at the hub. Consecutive radius modifications tended to occur on opposite sides of the hub in *Maymena* sp., presumably in order to balance tensions on the hub. After loosening all or most of the radii (and in some cases laying supplementary radii – next section), the spider simultaneously laid hub loops that connected all the radial lines, while at the same time she removed and ingested the loose fluff at the very center of the hub that had accumulated as a result of cut and reel behavior during elementary and supplementary radius construction. *Mysmena* sp. built only a single hub loop, while the others made 2-3 loops (Fig. O6.9). Hub replacement and reconstruction was nearly identical to the proto hub replacement behavior that occurs very early in orb construction in uloborids, but is probably not homologous with it (see, however, the discussion of homology below).

In some theridiosomatids the hub was removed entirely, and the radii were then fastened to each other in an “anastomizing” pattern (Shinkai and Shinkai 1985 on *Theridiosoma epeiroides*; Coddington 1986*a* on *T. gemmosum*). Other species then rebuilt a hub (McCook 1889, Coddington 1986*a*), as in some anapids (Eberhard 1987*c*). The four radii in the reduced “triangle orb” of *Hyptiotes* spp. (UL) were also reconnected in a similar pattern (Figs. 3.1, 10.23) so that they did not converge precisely on a single point. This is an independent derivation of the anastomizing pattern, which may serve to reduce the number of lines that the spider needs to grasp while she holds the web tight.

O6.3.8 Other modifications following sticky spiral completion

O6.3.8.1 Supplementary radii

O6.3.8.1.1 Uloborids: two enigmatic web types

Supplemental lines of one and perhaps two different types are also built by uloborid spiders. One type (“sheet orbs”) was discovered by Wiehle (1927) in the webs of second instar spiderlings of *Uloborus walckenaerius* and *Zosis* (= *Uloborus*) *geniculata*; the behavior used to build them was described later in *U. walckenaerius* and *U. plumipes* (Szlep 1961) and *U. diversus* (Eberhard 1977). The spiderlings built orbs, with typical radii, frames, a hub and a temporary spiral, but that lacked sticky spiral lines. After finishing the temporary spiral, which was unusually tightly spaced in *U. diversus* (Fig. 9.20) and also *U. plumipes*, the spider added a dense mat of extremely fine supplementary lines. These lines were so fine that they were nearly invisible, even when viewed under conditions (strong lighting from all sides and against a black background) under which the frame, radii and temporary spiral lines were clear (Fig. 9.20a); the supplementary lines became clear when coated with powder (Fig. 9.20b).

The behavior that the spider employed to add these “supplemental lines” is poorly understood. Immediately after finishing the temporary spiral the spider returned to the hub and began a long series of radial movements, out toward the frame and back to the hub. In *U. diversus* this behavior differed from typical radius construction in several details (Eberhard 1977). The spider often stopped before reaching the frame, attached her dragline to the radius and returned to the hub, apparently along the line she had just laid. She often tapped her abdomen against the line between one third and half way back to the the hub (presumably attaching a line or lines). She apparently broke and reeled the line running to the hub, and she released further dragline(s) so that she descended several mm; she then gradually reascended as she moved back to the hub, apparently reeling up the line in front as she laid new line(s) behind. A white mass gradually accumulated at the center of the hub as she made radial trips, presumably as a result of the loose silk that she reeled up this way. The spider made only a single attachment at the hub following each radial excursion, and did not turn slowly making hub attachments, or direct legs I or II laterally. Instead she simply turned when she reached the hub, seized the radii directly in front of her with both legs I, tapped or jerked quickly on these lines, and made another radial trip outward toward the frame.

Another difference was that each radial trip resulted in several new lines being added. This was confirmed by powdering webs just after supplementary line construction had begun; there were multiple lines in sectors where the spider had made only a single radial trip. In addition, consecutive supplemental radius trips were much closer together than were those in typical radius construction. In one typical sequence the orientations of successive trips by a *U. diversus* spiderling were toward 6, 5, 5, 3, 2, 1, 11, 11, 10, 10, 11, 11, 12, 9, 10 and 9 o'clock. One final contrast with typical orb construction was that U. diversus sometimes added supplementary lines on the night following original web construction.

In sum, the spider's behavior during the construction of supplemental lines differed from that during typical radius construction, and resembled radius construction behavior in araneids and tetragnathids and that just prior to proto-hub removal in uloborids, but was unique in some respects. It was also mysterious, because the orientations and numbers of lines added to the web did not correspond to the spider's behavior. Although many of the lines in a finished web were radially oriented, as would be expected from the radial movements of the spider, the webs also contained many very fine additional, non-radial lines (Fig. 9.20b). Many were relatively straight, and were parallel with each other in some cases. There were even some non-radial lines beyond the frame lines in webs of both *U. plumipes* (Szlep 1961) and *U. diversus,* even though spiders were not observed to go beyond the frame lines during construction (Eberhard 1977). The like conclusion is that some lines were floated on air currents during construction. If the currents were in consistent directions, they could explain the parallel orientations of supplementary lines.

The set of spiders that build these strange sheet-orbs offers further strange twists. Following their original discovery, "sheet orbs" have subsequently been seen in spiderlings of *U. plumipes* (Szlep 1961), *U. diversus* (Eberhard 1977), *U. trilineatus* and other *Uloborus* species (WE), *Philoponella vicina* (Peters 1953, 1955), and *P. arizonica* (Eberhard 1977). Similar dense sheet-orb webs were made by mature males of at least one *Uloborus* (Eberhard 1977) and *Philoponella tingena* (but only in some cases by those of *Zosis* spp. – see Fig. 3.48). The sheet-orbs of mature male *Uloborus* sp. differed from those of second instar spiderlings, in that they had typical uloborid hubs, with zig-zag radius-hub loop attachments, and lacked an accumulation of white, loose silk (Fig. 10.36c). The logical connection in this distribution is that both second instar spiderlings and mature males lack a functional cribellum, and thus cannot produce the sticky cribellum silk that forms the trapping portion of the typical orbs of other conspecifics (Wiehle 1927, Szlep 1961, Eberhard 1977). The fact that spiders abruptly began to build normal orbs with sticky spiral lines, whether or not they had had the experience of building sheet orbs (Szlep 1961), also makes sense, because the next instar has a functional cribellum.

But this explanation is incomplete in several respects. Some webs of later instar nymphs of U. plumipes and U. diversus were intermediate, with both cribellate spiral lines and temporary spiral and supplementary lines (Plate IV, Figs. 2a, b in Szlep 1961, Eberhard 1977); and some later instar of *U. plumipes* and *U. diversus* reverted to making sheet-orbs after having built typical orbs and then made further normal orbs (Szlep 1961). The resemblance between the sheet-orb webs of second instar and those of "senile" virgin females of *U. diversus* (Fig. 6.22, section 6.4, Eberhard 1971*b*) is also striking, but of unclear significance; the building behavior of senile individuals has never been observed directly.

Flexibility in sheet-orb construction construction was reflected at a higher taxonomic level in the uloborid genus *Conifaber*: mature females of one species (*C. parvus*) were seen only with sheet-orbs (Lubin et al. 1982; the sample was only 10-20 webs, however), while those of another (C. yasi) apparently make typical orbs with sticky spirals (Grismado 2008).

In sum, some uloborids made sheet-orbs even when they had a functional cribellum, for unknown reasons.

A final puzzling uloborid hub design that seems likely to be the result of modifications after the orb is otherwise complete occurred in the phylogenetically basal group *Waitkera waitkerensis*. Nearly every radius in one web had at least one "V" shaped pair of lines attached to it that appeared to originate in the outer portion of the hub (Fig. 10.17a,b, Opell 1999); this pattern has never been seen, to my knowledge in any other species. Other webs of this species (B. Opell unpub.), had either smaller numbers of these "V" shapes (Fig. 10.17c), or nearly completely lacked them (Fig. 10.17d). A few of these "V" lines were attached to hub loops rather than the radii.

O6.3.8.1.2 Symphytognathoids

Some tiny orb weavers constructed "supplemental" radii after finishing the sticky spiral, then loosened the previous, "elementary" radii to which the sticky spiral was attached. The taxonomic distribution of supplementary radii was somewhat irregular: they were built by several species in the anapid genus *Anapis,* were lacking in one species of *Anapisona,* and were present in some but not all webs of another. In mysmenids they were present in *Maymena* webs but absent in *Mysmena* webs; they occurred in the webs of the symphytognathid genus *Patu* (Lopardo et al. 2011). The spider built supplementary radii (which were of thinner silk lines than the typical or "elementary" radii) between these radii, using (as far as is known) the typical cut-and-reel radius construction behavior seen during elementary radius construction in these groups (Eberhard 1982, 1987*c*). The supplementary radii appeared to be laid under relatively low tension in *Maymena* sp.: the spider pulled additional line with her legs IV just before attaching each supplementary radius at the center. Consecutive supplementary radii tended to be laid by *Maymena* sp. on approximately opposite sides of the hub. No supplementary radii were laid above the plane of any horizontal orbs, and no hub loops were laid during supplementary radius construction.

After finishing supplementary radius construction, the spider broke and relaxed all of the radii, both elementary and supplemental. She repaired each elementary radius, attaching a line from its broken inner end to the center of the hub, but the broken inner ends of the supplementary raii were left free instead of being repaired. This left the supplementary radii under no tension at all in the finished web. These radii thus did not contribute mechanically to web stability under general stresses such as wind; perhaps they improved prey interception, stopping or retention by closing holes between the elementary radii.

O6.3.8.2 Silk stabilimentum construction

There is almost no information on the behavior immediately preceding stabilimentum construction, except in *U. diversus* (UL). In this species the orientation of the linear stabilimentum was non-random, tending to be place on a short radius attached near an anchor line and thus enabling spiders to make more rapid exits from the web when disturbed (Eberhard 1973a). The spider performed three different apparently sensory behaviors, including web-bouncing, and two types of flexing movements of her anterior legs, “slow flexes” and “sharp jerks” (Eberhard 1973a). Another uloborid, *Zosis geniculata*, also performed slow flexes, but no bounces and only occasional weak jerks just before building a stabilimentum line (WE).

The spider bounced the web by drawing her body downward, away from the web by flexing her legs ventrally, and then releasing the tension and swinging her abdomen upward, causing her body and the entire hub to swing upwards. Spiders often bounced several times, for up to 2-3 s; the frequency of the bounces was about 5/s in a mature female (probably the resonant frequency of the orb loaded with the spider’s weight). The slow flexes and sharp jerks were produced when the legs (especially legs I) flexed while they held radial or hub lines. Neither type of flexing was as vigorous as the otherwise similar movements that often preceeded attacks on prey. Typically, a spider performed a series of jerks, flexes and bounces while facing in one direction, turned and performed another series, and so on. There was no consistent order within a series. The spider often turned 90º or more between early bursts, but the turns gradually became smaller and smaller until all jerks and flexes were directed toward the same small sector of the orb where she then built the stabilimentum line. The positions of legs I during slow flexes and sharp jerks also changed gradually: legs I usually gripped adjacent or nearly adjacent radii early on, but later both gripped the same radius. The spider thus “zeroed in” on a particular radius with both her body and her legs just before she began to build a stabilimentum.

The behavior employed in building silk stabilimenta has been described in few species. *Uloborus diversus* (UL), *Zosis geniculata* (UL), *Micrathena duodecimspinosa* (AR), and *Gasteracantha cancriformis* (AR) used wrapping movements of the hind legs to lay swaths of silk against the web, often as the spider moved slowly forward (WE) (see also, for instance, McCook 1889, Wiehle 1927). *U. diversus* also dabbed her spinnerets against the web periodically (about every 5 mm) (Eberhard 1973), while *G. cancriformis* tended to dab at the beginning, wrap, and then dab again at the end of each short segment (tuft) of stabilimentum silk (WE). The uloborid *Z. geniculata* only dabbed her spinnerets against the web at the beginning and the end of a stabilimentum line, and repeatedly during construction of the thin central mat (WE, Fig. 3.46). The dabbing movements probably served to attach the stabilimentum silk to the radius or frame line with piriform attachment discs, but the stabilimentum silk of *Z. geniculata* and *U. diversus* also adhered to the web without attachment discs (Eberhard 1973). In contrast, *Argiope* spp. did not use their legs IV, and repeatedly dabbed their spinnerets directly against the web; a white swath of fine lines emerged from the spinnerets each time the abdomen pulled away (WE). Perhaps differences in details such as this were associated with convergent evolution of silk stabilimenta in different lineages (Herberstein et al. 2000b).

O6.3.8.3 Orb destruction and repair

Web removal by the rapid “curtain” technique and the slower, sector by sector “snow plow” method was reported in several araneid genera by Carico (1986). Snow-plow web removal also occurred in Leucauge mariana (TET) and Nephila clavipes (NE), just before or as the first drops of a coming rain storm fell (WE). In some cases the spider removed some sectors but left others intact as the rain came. Presumably removal behavior in this context avoided loss of glue, which would be washed off lines by rain.

Further details of major, “replacement” repairs (replacing damaged sticky lines with new sticky and non-sticky lines – section 6.3.8), included the following in uloborids and nephilids. The first stage of replacement repair in U. diversus (Eberhard 1972) resembled a shoring up repair. The spider walked along the sides of the damaged area more or less parallel with radii, and packed together the loose lines. In some but not all cases she then discarded this silk. She attached her drag line as she moved to other lines that she had already laid in shoring up repairs and to other non-sticky lines in the border of the hole. Then, after resting at the hub, she began to replace the damaged sector by laying radial lines from the broken edge of the hub to the exterior border of the hole or, when an entire sector was being replaced, to the replacement frame (Fig. 6.18a$_3$). She used the radii at the edges of the hole as exit radii, and moved laterally along the far edge of the hole to find a non-sticky line (usually a broken radius) to which to attach her dragline. After laying several replacement radii, the spider began to destroy the old hub. She attached her drag line to the point where the new radii that she had just built converged, which became the center of the new hub; she then repeatedly cut away sectors of the old hub. She moved one or a few body lengths away and attached her drag line to the radius that she had just cut, and returned to the new hub. She repeated this process until the old hub was entirely removed. This behavior, which resembled replacement of radial lines near the proto-hub during orb construction (section O6.3.5.3), resulted in several short new radii that ran across the open space where the old hub had been, and that were attached to the inner ends of the radii in the remaining intact portion of her orb. The spider was now in a situation very similar to that following proto-hub removal in normal orb construction, and subsequent construction behavior (adding further radii and hub, temporary spiral, and sticky spiral) was not distinguishable from usual whole orb construction.

Examinations of finished repaired orbs of N. clavipes (NE) and Z. geniculata (UL) suggest that they performed similar sequences of repair behavior, though no direct observations of behavior are available. The hub of *N. clavipes* was also apparently consistently modified as part of replacement repair (Fig. 1 of Nentwig and Spiegel 1986), but close examination showed that it usually differed from *U. diversus* in that it was often only partially replaced (Fig. O6.10). *Zosis geniculata* sometimes made somewhat similar repairs, in which the spider removed or at least collapsed only part of the hub before building new radii (WE).

Rarely *U. diversus* performed a second, "false hub" type of replacement repair, in which a second, incomplete hub was built along the outer edge of the broken sector (Fig. 6.18). The behavior employed to execute false hub repair was only observed once (Eberhard 1972). The spider did not cut away old threads; instead she built the new radii that originated from a small area along the edge of the old web. This type of repair was performed almost exclusively by relatively old, "senile" females (Eberhard 1972) (section 6.4). These repairs bore an uncanny resemblance to the pseudo-orb webs of the amaurobiid *Titanoeca albomaculata* (Fig. 10.14, Szlep 1966a) and the psechrid *Fenecia* spp. (Fig. 9.18) (Bayer 2011, Agnarsson et al. 2013). Unfortunately, web construction behavior has never been observed in detail in any of these groups, so further comparisons cannot be made.

A quite different replacement repair behavior was performed by an individual of *C. confusa* (Shinkai 1998). The spider did not remove and replace the hub, but rather added new hub lines as she laid new radii that originated in or very near the old hub (Fig. O6.5a). She zig-zagged back and forth in the outer portion of the orb while she laid both the temporary spiral and the sticky spiral, turning back at or near the edge of the repaired sector. But nearer the hub she circled the web completely with both temporary spiral and sticky spiral lines. The mechanism(s) by which the spider guided herself to produce these nearly circular loops in the absence of the usual cues from the outer loop of the temporary spiral and the inner loop of the sticky spiral (section 7.3.2) is unknown (see also Fig. 7.36).

O9 Case studies of possible functions of diverse, convergent web designs

O9.1 Tangles near orbs

Various unrelated orb-weaver species built tangles of non-sticky silk near their orbs (Figs. 10.3, O9.1, Table 3.6)). Tangles were built in several different postions with respect to orbs, and reflected in miniature the grand themes of diversity and rampant evolutionary convergence in Chapter 9. Based on the phylogenies of Coddington 1990, Scharff and Coddington (1997) and Kuntner et al. (2008a), tangles adjacent to orbs have arisen in orb weavers at least 11 different times. Studies documenting the probable functions of tangles near orbs (Table 3.6) suggest that they probably have several non-exclusive functions, including defense against predators, prey interception, prey retention, web stabilization, and perhaps even prey attraction.

The most common function for tangles was probably to defend the spider from diurnal, flying or jumping predators. In addition to forming a physical barrier, tangles also served an early warning function; contact with the tangle of *Argiope trifasciata* (AR) induced the spider to perform defensive behavior (Tolbert 1975) (see also Lubin et al. 1982). Another line of indirect evidence favoring the defense hypothesis is that all orbs with tangle were operated during the day, when many of the predators of orb weavers (birds, lizards, wasps, odonates, jumping spiders, etc.) are also active. The spider rested at the hub during the day, rather than at the edge or off of the web in nearly all species that built a tangle at the side or below the orb. The exceptions, in which the spider rests away from the hub, also support the defense hypothesis, because the tangle was around the spider's retreat, as in *Araneus omnicolor* (AR), *Metepeira* spp. (AR), and *Chrysometa* spp. (TET) (Tables 3.6). To my knowledge, there is no species in which there is a tangle built alongside the orb and the orb is up only at night; nor are there any exceptions to the rule for the tane to be near the site where the spider rested during the day (Table 3.6).

Further evidence favoring the defense hypothesis was that when the tangle was on only one side of a more or less vetical orb, it was always on the same side on which the spider tended to rest (i.e., the tangle was on the lower side of slanting orbs in which the spider rested under the hub). This trend occurred in several *Argiope* species (AR) (Hingston 1932; Lubin 1975; Tolbert 1975; Eberhard 2013), *Nephila clavipes* (NE) (Higgins 1992), and *Allocyclosa bifurca* (AR) (WE). When there were tangles on both sides of vertical orbs, the tangle on the spider's side was usually denser in *N. clavipes* (Higgins 1992), and *A. trifasciata* (Tolbert 1975 and WE). The most extensive data showed that in 3237 orbs of *N. pilipes* (= *maculata*) (NE), 640 had barrier tangles; 94.8% were below the orb (the side on which the spider rested), 5.2% were both above and below; none were only above the orb (Robinson and Robinson 1973*a*). In some species such as *N. pilipes* (Robinson and Robinson 1973*a*), *N. clavipes* (Higgins 1992, WE), and *Argiope trifasciata* (AR) (Tolbert 1975, Eberhard 2013), in which the tangle was smaller than the orb, it was more or less centered on the hub, where the spider rested during the day.

The defensive behavior of some spiders with tangles was also appropriate to exploit the protection offered by barrier webs. Nymphs of *N. clavipes* (NE) remained at the hub but shifted to the opposite side when a damselfy made repeated strikes at them through the tangle; it dropped to the ground when a bird struck (Higgins 1992). *Uloborus conus* and *Conifaber parvus* dropped on a short line below the hubs of their horizontal orbs to hang inside the cone-shaped tangle immediately below when they were disturbed; *U. conus* also dropped below the hub, and often bounced, when the hub was in direct sunlight (Lubin et al. 1982). *Leucauge mariana* dropped in the same way and hung in the midst of the sparse tangle below her orb when a parasitoid ichneumonid wasp, *Hymenoepimecis tedfordi,* struck at her from above the hub but failed to grab her (WE).

Still further indications of a defensive function are the changes in the relative frequency with which tangles were built next to the orbs of nymphs of *N. clavipes* of different sizes, because tangles were correlated with the frequency with which attacks were observed on individuals of different sizes (Higgins 1992). In *Uloborus trilineatus* (UL), the presence of a cone-shaped tangle below the orb was associated with an imminent moult, a particularly dangerous stage when the spider is defenseless (Lubin et al. 1982). Finally, direct observations of failed attacks on *N. clavipes* have confirmed that attacks by birds and by giant damselflies which are specialist predators on spiders in their webs were sometimes impeded by tangles (Higgins 1992, Fincke 1992, Tseng et al. 2011).

Even here, however, diversity defeats simple generalizations. There was at least one predator that actually *exploited* tangles to capture orb weavers. The emesine bug *Stenolemus giraffa* climbed stealthily into the tangle near the orb of the spider *Argiope katherini* while the spider rested at the hub, and was thus able to approach to within striking range for its raptorial front legs (Soley et al. 2011, F. Soley, pers. comm.).

The variety and ubiquity of defensive structures such as twigs, suspended curled leaves, etc. in theridiid webs and these theridiids' tendency to rest on or under these objects during the day, offer further testimony to apparent strength and widespread nature of selection to defend against predators (Eberhard et al. 2008*a*). Blackledge et al. (2003) argued that a further indication of a defensive function for the tangles of theridiid webs against predatory sphecid wasps was that theridiids were apparently under-represented in prey lists of sphecids. It is difficult to evaluate this argument, however, because there are no data regarding the real availability of theridiids to hunting sphecids.

Linyphiids contrasted dramatically with theridiids, as they only seldom incorperated foreign objects such as plant debris and prey remains in the web and used them as resting sites (e.g., Nielsen 1932; Comstock 1967). Linyphiids may have instead derived protection from the tangles near their sheets, although tangles were absent in some groups. Species that rested in the middle of horizontal sheets (including species of *Neriene*, *Frontinella*, and *Orsonwelles*) may have had more extensive tangles below the sheet than those which rested at or just beyond the edge of the sheet (e.g. under a nearby leaf) (*Agyneta* [= *Meioneta*) spp. *Mermessus* [= *Eperigone*] *tridentatus, Labella thoracica* Nielsen 1932, *Australolinyphia remota, Bathyphantes pallidus, Floronia bucculenta, Dubiaranea lububris, Neomaso patagiatus,* and

Ostearius melanopygius (Hormiga and Eberhard in prep.) (some of these lacked tangles entirely, or had only sparse tangles). Further, more quantitative comparisons are needed.

With respect to horizontal orbs, dense tangles above the orb may often function to intercept flying insects and knock them down onto the orb, just as the tangles of many non-orb families such as Agelenidae, Tengellidae, Linyphiidae, Pholcidae, Dipluridae are thought to knock flying prey onto their sheet webs (e.g. Kaston 1964). Prey retention is probably an additional function in such tangles that also include sticky lines, as in *Philoponella oweni* (Fig. 1.6). These sticky lines resembled those in tangles above the sheets of some non-orb weavers such as *Tengella radiata* (Fig. 10.7) (Eberhard et al. 1993) and various linyphiids (Benjamin et al. 2002, Benjamin and Zschokke 2004). Geometrically regular rather than tangled arrays of sticky lines are built just above horizontal orbs by some symphytognathoids (Figs. 7.9, 3.32; Lopardo et al. 2011), and presumably also function to intercept, knock down, and retain prey.

Tangles have further functions in some species with horizontal orbs. In *Cyrtophora citricola* (AR) the tangle above the horizontal orb of non-sticky radial and temporary spiral lines (Fig. 1.7) is much the denser than the tangle below (e.g. Wiehle 1928, Kullmann 1958), and is attached in many places to the orb's upper surface (Fig. 1.7), as is also true in some aerial theridiid sheet webs (Jörger and Eberhard 2006, Barrantes and Weng 2006, Madrigal-Brenes and Barrantes 2009) and many linyphiid sheet plus tangle webs (Hormiga & Eberhard in prep.). The tangle below the orb of *C. citricola*, in contrast, is less dense and is especially sparse in the space just below the orb, to which it is attached by only a few lines which produce downward-directed "pimples" in the orb. A similar reduced density just under the sheet and downward-directed pimples also occurs in theridiids such as *Chrosiothes portalensis*, *Nihonhimea* (= *Achaearanea*) *tesselata* and *C*. sp. nr. *porteri* with dense sheets (Eberhard et al. 2008*a*), many linyphiids (Nielsen 1932, Suter 1984), and the diguetid *Diguetia albolineata* (Fig. 9.16g) (Eberhard 1967). The open space just under the orb or sheet probably serves to allow the spider to run rapidly under the sheet to attack prey.

Still another possibility is that tangles stabilize orbs against general stresses produced by wind. Tangles were about twice as common in Argiope argentata (AR) webs at a windy site than at a nearby protected site (Lubin 1975). Younger nymphs of the tetragnathid Leucauge argyra, whose web lines were thinner and weaker than those of adults, had dense tangles above their more or less horizontal orbs; the tangle was connected to the hub of orb, pulling it up into a shallow cone (Fig. 10.3) (Triana-Cambronero et al. 2011). When the lines from the tangle to the hub were cut, the orb sagged more substantially when it was blown on; wind produced damage in the field by causing slack sticky spiral lines to come into contact and adhere to each other, leading the authors to conclude that the tangle functions to stabilize the orb. The tangle is less dense in the webs of older instar nymphs, and was completely absent in adult webs.

Still another, non-exclusive possibility is that barrier webs aid in prey capture by having a "ricochet" effect that causes prey to blunder into the orb, as has been observed in webs of social species (Lubin 1974, Uetz 1989), or by slowing the flight of fast-moving prey enough to allow them to be stopped when they bounce off the tangle into an orb. The likelihood of ricochet and slowing effects is uncertain. First, and most directly, experimental removal of barrier tangles from the webs of *Nephila clavata* (NE) and *Thelacantha brevispina* (AR) resulted in increased rather than decreased prey interception by the orb, as recorded by video cameras mounted beside webs in the field (Blamires et al. 2010*b*, Tseng et al. 2011). Inclusion of retention after the prey stayed in the orb for > 5s in the *N. clavata* analyses showed that captures were also higher when the barrier was absent ("O" vs. "B" treatments of Blamires et al. 2010*b*), arguing against the ricochet and slowing hypotheses. Some prey flying in the vicinity of the orb are presumably intercepted by the tangle and then fall or otherwise escape before they encounter the sticky lines of the orb. There may thus be both positive defensive payoffs that are substantial enough to compensate for the reduced prey capture in some species with tangles.

Finally, there is the possibility that the sparse tangle that is built to one side of the more or less vertical orb of *T. brevispina* (AR) attracts prey via the conspicuous tufts of white silk that are added to the tangle (Tseng et al. 2011). The data on prey capture effects from two years were contradictory, however (the prey attraction hypothesis for white silk decorations is discussed in sections 3.3.4.2).

In summary, tangles accompanying orbs have evolved repeatedly, and have diverse structures and functions. One remaining mystery is why the frequency of tangles varies so dramatically during the spider's lifetime in species such as *L. argyra* (Triana-Cambronero et al. 2011), *L. mariana* (Maroto 1981, Barrantes et al. 2017), and *Argiope trifasciata* (Tolbert 1975). In *A. trifasciata,* for instance, 100% of all juvenile webs (including those of 39 penultimate females) had tangles, but only 3.4% of 29 adult webs had tangles. Tolbert (1975) speculated that barriers may be omitted when the body size of the spider becomes too large for salticid spider predators (which he observed attacking them), but there are no further data to substantiate this.

O9.2 Webs made by mature males

Most male spiders turn into sex machines when they reach maturity. They cease spinning webs, and spend their time searching for and wooing females, and in some cases fighting with other males (Schuck-Paim 2007). The primacy of sex over food is epitomized by males of the linyphiid *Linyphia triangularis,* in which the male initiates cohabitation with a female by tearing down her prey capture web (thus removing a source of female pheromone which can lure other males) (Rovner 1968). Mature males of a few distantly related species resort, however, to web robbery. They drive immature conspecific nymphs from their orbs, and capture and feed on prey there in the *Nephila clavipes* (NE) (Christenson 1990), *Metazygia gregalis* (AR) (Eberhard et al. 1978), *Larinia directa* (AR) (Eberhard et al. 1978), *Eustala fuscovittata* (Eberhard et al. 1978), and *Tetragnatha* sp (Eberhard et al. 1978), *Leucauge mariana* and *L. argyra* (TET) (WE), and *Philoponella republicana* (UL) (Lubin 1980). Other mature males allow the female to remain in the web, but steal at least some of the prey captured there, as in *Frontinella pyramitela* (LINY) (Hirscheimer and Suter 1985) and pholcids in the genus *Modisimus* (Eberhard and Briceño 1983).

In a few scattered species, the mature male constructed a web of his own. Some male webs, such as those of the diplurid *Linothele* sp. (Paz 1988), several uloborid genera (Eberhard 1977, Lubin 1986), and the lycosid *Aglaoctenus castaneus* (Eberhard & Hazzi in press) were designed for prey capture. Other skeletal "resting webs" apparently served as protected structures where males rested during the day (Fig. 10.36). The general lack of sticky silk in resting webs indicates that they do not capture any prey. One mature male of *Uloborus bispiralis* (UL) was found on a small orb with a defensive cone-shaped tangle below that lacked sticky lines (Lubin et al. 1982), and one of 34 adult male *Metepeira gressa* (AR) built a rudimentary orb with a few sticky lines (Viera 1988). Many other mature males simply rely on camouflage; web-less males may be especially subject to attack by predators (Pasquet et al. 2007 on the araneid *Z. x-notata*).

Still other males in a wide variety of species have convergently evolved to build prey capture webs (Fig. O9.2, Table 10.5). There is also some within-taxon diversity (for example, mature male of the pholcid *Holocnemus pluchei* do not build webs of their own but instead invade those of conspecifics (Jakob et al. 1998), while those of three other pholcid genera make their own webs (Table 10.5). Males of the pholcid genus *Modisimus* may use web construction "chivalrously" ceding prey to her to induce the female to stay with him, where he can defend her from other males (Eberhard and Briceño 1983) (the dense populations of *H. pluchei*, whose males do not cede prey go females, may make defense of the female more difficult) (Blanchong et al. 1995). In the linyphiid *Frontinella pyramitela* only young mature males (up to 11 days after the final molt) make prey capture webs (Suter et al. 1987); the additional weight they gain from feeding at this time may improve their fighting success in subsequent battles with other males over females (Herscheimer and Suter 1985). Mature male webs seem especially common in the symphytognathoid familes of tiny orb weavers Anapidae and Mysmenidae, where it may be the rule rather than the exception that mature males make fully functional sticky prey capture webs (Table 10.5, Eberhard 2007, Lopardo et al. 2011). The orb webs of mature male *Anapisona simoni* (AN) were not distinguishable from those of mature females (Eberhard 2007, WE).

There are also mixed male strategies, in which the large majority of mature males lacked webs but a few were on tiny webs (*Erigone* sp. – Alderweireldt 1994, Thornhill 1983). At least in *Erigone* sp., spiders sometimes also captured prey without building a web, suggesting multiple alternative prey capture tactics (Alderweireldt 1994).

Mature orbicularian males are generally thought to lack the aggregate and filiform and cribellum glands that produce sticky silk, and there may be an associated trend for mature males of species in which sticky silk is sparse (*Wendilgarda* sp., Eberhard 2000) or absent as in *Cyrtophora citricola* (Fig. O9.2), *Manogea porracea* (Sobczak et al. 2009), and *Mecynogea* sp. (João Vasconcellos-Neto, pers. comm.) to recover the ability to build prey-capture webs. The webs of mature male uloborids in the genera *Uloborus* and *Philoponella* emphasize this trend to use non-sticky lines, as they revert to the web design of early nymphs, which lack sticky silk because the nymph lacks a functional cribellum (Szlep 1961, Eberhard 1977*a*, Lubin 1986). A similar adjustment occurs in the non-orb theridiid *Theridium evexum*, but it is only partial: mature males steal webs from smaller nymphs, but their wrapping silk has sticky droplets, thought they appeared to be smaller and less abundant (G. Barrantes, pers. comm.).

The multiple convergences on stealing webs from nymphs, and on the construction of webs by mature males, intimate that web construction and prey capture by mature males may be advantageous in other groups where it does not occur. Perhaps it has not evolved in some groups due to constraints placed on males by the loss of the ability to produce sticky silk. This constraint argument is not very appealing, however, because the males of these groups made webs with completely functional sticky lines only one instar earlier. Analyses of the costs and the benefits of web construction seem more likely to illuminate this question. The benefits of trapping webs would seem greatest for males of species in which long life is especially important and feasible, for instance when females are particularly difficult to find (e.g. in sparse populations), or when mortality factors such as predation are especially low. The widespread occurrence of prey capture webs in symphytognathoids (Table 10.5, Lopardo et al. 2011) intimates that (surprisingly) the males of these tiny litter spiders have relatively long lives. I know of no data to test any of these hypotheses.

In sum, the twin themes of striking diversity and frequent convergence are illustrated once again in the webs built by mature males of orb weaving species.

O9.3 Angle of the web plane with horizontal

Orbs were diverse with respect to the angle that the plane of the web makes with horizontal (the "slant"); it ranged from nearly perfectly horizontal to nearly perfectly vertical (Table O3.1). Again both diversity and convergence are rampant, and simplistic characterizations such as vertical orbs in araneids and horizontal orbs in tetragnathids had many exceptions. For instance, the araneid *Colphepeira catawba* (Bradley 2013) had horizontal orbs, while tetragnathids such as *Meta ovalis*, *Tetragnatha laboriosa*, *T.* sp., and *Metellina mimetoides* at least sometimes built vertical orbs (Bradley 2013, WE). Orientations also vary even between closely related species: the means for the uloborids *Philoponella arizonica* and *P. oweni* were 6.8±13.8° vs 51.0±24.2° (Smith 1997). Slants in some genera, however, appeared to be relatively constant, especially those that are close to 90° and to 0°. Intra-specific variation were also sometimes huge. To cite three extreme cases, the slants of the orb of the araneid *Poltys noblei* averaged 30°, but ranged from horizontal to vertical (Smith 2006); the same individual of the araneid *Neoscona nautica* sometimes built a vertical orb one day and a horizontal one the next (Edmunds 1978); and young *Paraneus cyrtoscapus* built horizontal orbs while adults made vertical orbs (Edmunds 1978) (see also Bradley 2013 on *M. ovalis* and *T. laboriosa*). On the other hand, many species had relatively consistent slants. For example, an unusually long series of measurements of *Metepeira gressa* gave means and standard deviations of 76±7° for 67 adults, and 75±6° for 84 juveniles (Viera 1989, 2008).

Counting those species in Table O3.1 with samples of at least 5, slants that were consistently nearly perfectly vertical occurred in araneids scattered across the araneid tree (e.g., Fig. 1.12), including most (but not all) *Cyclosa*, *Allocyclosa*, *Wagneriana*, *Scoloderus*, some *Alpaida* (but not others), some *Araneus* (but not others), *Eriophora*, some *Eustala* (but not others), and *Verrucosa*. Judging by other published verbal descriptions (rather than numerical data), the ladder web *Tylorida* sp. (TET) (Robinson and Robinson 1972), *Deliochus* sp. (AR)

(Kuntner et al. 2008a), the trunk orb species *Telaprocera* sp. (AR) (Harmer 2009), and *Cryptaranea atrihaustula* (AR) (Forster and Forster 1985), *Eustala conformans* and *E. perfida* (AR) (Messas et al. subm., WE), and *Herrenia* spp. and *Clitaetra* (NE) (Kuntner et al. 2008a) also built nearly perfectly vertical orbs. More nearly vertical orbs probably have both advantages and disadvantages (section 4.9.4) (Table O3.1). Similarly, more or less horizontal orbs also appear convergently in scattered branches of araneoids (the areneids *Azilia affinis*, *Mangora* spp., *Enacrosoma anomala*, the symphytognathoid families, most tetragnathids (Table O3.1).

One large survey (WE) suggests that orb slants may be conveniently grouped in five different general classes (Table O3.1): A) consistently very close to vertical (e.g., the genera just mentioned; these webs are perhaps especially effective against moths, as in *Scoloderus* spp. and *Tylorida* sp., and in allowing the spider to build against tree trunks, as in *Herrenia* and *Telaprocera*); B) close to vertical but generally >5^o from perfectly vertical (e.g., 50 – 90^o for the vertical orbs of *Paraneus cyrtoscapa* (Edmunds 1978), means of 70-80^o for *Argiope trifasciata* (Ramírez et al. 2003), *Eustala* spp., *Alpaida acuta, Acacesia hemata*, *Argiope* spp., *Chrysometa alboguttata*, *Pronous wixoides*, and *Metepeira* spp.); C) substantially less than vertical, but generally more than 45^o (*Philoponella oweni* (Smith 1997), all *Gasteracantha* and *Micrathena* characterized to date, *Mangora pia, Alpaida veniliae, Witica crassicauda,* and *Philoponella tengena*); D) occasionally close to horizontal but more often 20-40^o (e.g., *Leucauge* spp., *Mangora melanocephala* (and probably other congeneric species), and *Spilasma duodecimguttata*; and E) usually not more than 20^o from horizontal (*Philoponella arizonica* (Smith 1997), *Uloborus trilineatus, Zosis, Dolichognatha* spp., *Metabus ocellatus,* and most (but not all) *Tetragnatha*).

Species in categories A-C have often been characterized as building “vertical” orbs, those in D and E as building “horizontal” orbs (section 1.7). The distinction between A and B is functionally important, because A webs present greater problems for the spider in moving around the web and greater damage when the spider moves across the finished web, but probably give greater prey retention times, as the prey more frequently “tumbles” into contact with additional lines as it struggles in the web (Eberhard 1989, Zschokke and Nakata 2015), and less damage from falling detritus which also needs to be removed (Pasquet et al. 2007). Having an orientation very close to 0^o (class E) may also be important in getting the orb into a spatially limited zone where prey are particularly abundant. Possible examples are the tetragnathids *Metabus ocellatus* which builds just above the surface of streams (Buskirk 1975) and *Glenognatha heleois* which builds just above marshy ground (Hormiga and Döbel 1990).

In sum, the slants of orbs show the same pattern of substantial diversity and frequent convergence seen in other web traits. The slants of non-sticky sheets, in contrast, hovered around 0^o, probably to reduce the chances of prey falling off of the sheet before the spider arrived to attack it.

O9.4 Special spinneret morphology that facilitates moulting on a web

Araneomorph spiders have solved one futher problem related to webs in an elegant way. Mygalomorph spiders make a silk sheet just prior to moulting, often at the bottom of a burrow, on which the spider then lies with her legs projecting upward while she moults. In contrast, moulting is more aerial in most araneomorphs: the spider grasps silk lines with her tarsi, or dangles free in the air, suspended at the end of a dragline by her spinnerets (e.g., Foelix 2011). But aerial moulting in which the spider spins lines just prior to molting is morphologically tricky: the new cuticle forms just below the old, soon-to-be discarded cuticle, and thus lies between the spigots on the old cuticle and the silk glands inside the spider’s abdomen (Townley and Tillinghast 2009). The spider succeeds in producing lines during and just before moulting by maintaining a connection between some of her silk glands and their spigots on the old cuticle. The connection is achieved by forming collared openings in the new cuticle, through which the ducts of the glands run to the old spigots. When the old cuticle is shed, these collared pores (termed “tartipores”) collapse and close. Tartipores are known in a variety of mygalomorph and areneomorph spiders (Griswold et al. 2005; Townley and Tillinghast 2009). Neocribellate araneomorphs have tartipores for major and minor ampullate, and even for piriform and aciniform glands (Griswold et al. 2005). It seems likely that the existence of tartipores facilitated the evolution of life styles in which moulting could occur independent of sheltered cavities.

There may be more to this story, as tartipores are absent in some groups (e.g., most haplogynes) for reasons that are not clear (perhaps haplogynes become more completely independent of silk just prior to moulting than other spiders?). There are also as yet unexplained evolutionary and ontogenetic changes in which individual glands are provided or not provided with tartipores (Townley and Tillinghast 2009).

O10 Final thoughts and future research

Table O10.1 lists some of the many unresolved problems that require further data. Future researchers will undoubtedly be guided by their own interests rather than any particular ideas of mine, but I hope that the general over-view of studies of spider webs that I have acquired in writing this book may help others find some potentially fruitful general research areas.

One general theme in Table O10.1 (points 1-4), is the need for arachnologists who study webs to be more alert to the natural contexts in which the webs they study evolved. The level of “ecological realism” in any given set of observations can impose limits on the kinds of conclusions that can reasonably drawn. Determining these limits in lab studies and even from observations made under current “field” conditions is not always easy. For instance, just because spiders are studied out of doors where they are free to move into and out of the study area does not guarantee that the observations will provide reliable information on the conditions under which their web designs *evolved*. I m confident, for instance, that the araneid *Metazygia gregalis* did not evolve in large open, uniform (periodically mowed) fields of grass and weeds such as the one in which my students and I studied them and their prey (Chacón and Eberhard 1980, Eberhard et al. 1978, Castillo and Eberhard 1983). I am equally certain that *Zygiella x-notata* and *Larinioides* (= *Araneus*) *cornutus* did not evolve building webs against large glass windows, and that neither the indenties nor the behavior of the prey that they capture there (Venner and Casas 2005) nor the wasp predation bought on by their high visibility of the spiders and their retreats against the white frames of such windows (Eberhard

1970) that were documented in such study settings are realistic ecologically. Ecological realism is an important consideration if one wishes to understand spider and their webs in terms of natural selection. On the other hand, observation of some kinds of behavioral details, such as how different legs are used during orb construction, are probably completely adequate in terms of their ecological realism even when observed in captivity. It is necessary to think carefully in judging the importance of ecological realism.

In this same vein, observations of unrestrained insects flying near webs in the field will be needed to answer the important questions raised by Craig (1986) regarding whether the clear evidence that insects can avoid orb webs in well-lit, visually simple laboratory settings (e.g. Fig. 3.2) (which led her to wonder why any insects are ever captured by webs), is representative of what occurs under more natural conditions. One technical breakthrough that promises to help in accumulating field observations of the behavior of both prey and predators of web weavers, is using portable video cameras to record events continuously at a web, a technique pioneered by I.-M. Tso and his associates. Further exploitation of this technique, especially with the cheaper and more resistant cameras that are now available, may help solve several long-standing problems.

A second general theme that is related to several topics mentioned in Table O10.1 concerns the recent explosion of studies that have documented a hitherto unsuspected inter-specific, intra-specific, and even intra-individual variation in the composition and the mechanical properties of silk from homologous glands. As noted by Blackledge et al. (2011), determining the degree of correlation (and lack of correlation) between such changes and differences in web designs and the possible advantages of the correlations is one of the most exciting frontiers of spider web biology.

Table O2.1. Lines grasped by the spider's tarsi in orb-weavers waiting at the hubs of orbs when the spider was apparently "alert" for prey (she was apparently not frightened into crouching, or aligning her anterior legs in a constrained, presumably camouflaged posture). The data are from an arbitrarily chosen sample of published photographs; they are preliminary because in nearly all the species other than those that I have observed myself, they were from only one (or at most a few) photographs. Some species were not entirely consistent in grasping the same lines with the same legs. For instance, in 28 individuals of the tetragnathid *Leucauge mariana* photographed in the field, one leg I grasped a hub loop rather than a radius in 1.8% of the cases, and one leg III grasped the hub's inner edge rather than a hub line in 7.1% (Briceño and Eberhard 2011) (fz = free zone; cz = capture zone; ie = inner edge of the hub; oe = outer edge of the hub; h = hub lines including radial or spiral lines that were neither the inner nor the outer edge of the hub; a = in the air (held no line); l = line out of the plane of the web; "/" indicates inconsistent placements of the left and right legs, or in different photos of the same species).

Taxon	Leg I	Leg II	Leg III	Leg IV	Reference
Tetragnathidae					
Cyrtognatha rucilla	fz	fz(?)	h	h	Dimitrov et al. 2007
Azilia affinis	fz	fz	h	h	WE
Leucauge argya	fz	fz	h	h	WE
L. blanda	fz	fz	h	h	Shinkai and Takano 1984
L. mariana	fz/cz	fz	h/ie	h/ie	Briceño and Eberhard 2011
L. magnifica	fz	fz	h/ie	oe/h	Shinkai 1989, Shinkai and Takano 1984
L. subblanda	fz?	fz?	oe?	h (ie?)	Shinkai and Takano 1984
L. venusta	fz	fz	h	h	Dimitrov and Hormiga 2010
Meta menardi	fz[1]	fz[1]	h	h(ie?)	Shinkai and Takano 1984
Metabus ocellatus	fz	fz	h(oe)[2]	h(oe)[2]	WE, Álvarez-Padilla and Hormiga 2011
T. pinicola	fz	fz	h	h	Shinkai and Takano 1984
T. praedonia	fz	fz	?[3]	h	Shinkai 1989
Nephilidae					
Nephila clavipes	h/cz	h/cz	h	h	WE
N. clavata	cz	cz/fz	h	h	Shinkai and Takano 1984
N. pilipes	h	h/cz	h	h?	Robinson and Robinson 1973a
Araneidae					
Allocyclosa bifurca	h	h	h	h	WE
Araneus cornutus	h/oe?	h/oe?	H	h	Shinkai and Takano 1984
A. marmoreus	h	h/oe?	h/oe	h	Shinkai and Takano 1984
A. stella (= *tsuno*)	h	h	?	oe/fz?	Shinkai and Takano 1984
A. uyemurai	h	h	h(oe?)	h/oe	Shinkai and Takano 1984
A. ventricosus	oe	h/oe	h	h	Shinkai and Takano 1984
Araniella displicata	h	h	h	h	Shinkai and Takano 1984
Argiope aemula	?	?	h	h	Shinkai and Takano 1984
A. argentata	h	h	h	h	WE
A. boesenbergi	h	h	h	h	Shinkai and Takano 1984
A. minuta	?	?	h	h	Shinkai and Takano 1984
A. savygnii	h	h	h	h	WE
Cyclosa atrata	h	h	h	h	Shinkai and Takano 1984
C. camelodes	h[4]	h[4]	h[4]	h[4]	Shinkai and Takano 1984
C. ginnaga	h	h	h	h	Shinkai and Takano 1984
C. japonica	h[4]	h[4]	h[4]	h[4]	Shinkai and Takano 1984
C. laticauda	h	h	h	h	Shinkai and Takano 1984
C. monticola	h	h	h	h	Shinkai and Takano 1984
Deliochus sp.	h	h	h/ie	h	Fig. 3.5, Kuntner et al. 2008a
Larinia argiopiformis	h	h	h	h	Shinkai and Takano 1984
Metazygia wittfeldae (?)	oe/fz	h	h	h	WE
Micrathena duodecimspinosa	a	h/ie	h/ie	h/ie	WE
M. horrida	a	ie	ie	ie	WE
M. sp. nr. *lucasi*	h	h/ie	ie	ie	WE
Neoscona adianta (= *doenitzi*)	?	h	h	h	Shinkai and Takano 1984
N. scylla	h	h	h	h	Shinkai and Takano 1984
Plebs (= *Zilla*) *aurea*	h	h	h	h	Shinkai and Takano 1984
Poltys illepidus	h(oe?)	h	h	h	Shinkai and Takano 1984
P. laciniosus	h	h	h	h	Smith 2006

Zilla astridae	h	h	h/ie	h	Shinkai and Takano 1984
Zygiella montana	h	h	h	?	Shinkai and Takano 1984
Theridiosomatidae					
Epeirotypus sp.	l	l	?	h	Coddington 1986*a*, WE
Uloboridae					
Philoponella vicina	h	h	h	h	WE
Uloborus diversus	h	h	h	h	WE
U. sp. nr. triline*atus*	h	h	h	h	WE
Zosis geniculata	h	h	h	h	WE

[1] tarsi are surely beyond the outer edge of the hub; they may be beyond the free zone and within the capture zone, but the photo is not clear on this point

[2] sometimes holds the outer edge, sometimes not (Fig. 2.19)

[3] presumably h or oe, but the lines are not visible in the photograph

[4] clear from the photograph that all of the legs of the crouching spider are too short to reach lines beyond the edge of the hub

Table O2.2. A tentative list of possible deep uniformities in two details of leg movements, following, and prolateral vs retrolateral short-distance shearching movements, that are performed during orb construction by a serendipitous sample of species whose construction behavior I happen to have recorded (not all stages are represented for all species). All recordings were made in the field except those of *Cyclosa monteverdi, Nephila clavipes,* and *Zosis geniculata*. In most species only a single individual was filmed, but in all cases the activity was repeated many times. Sticky spiral construction was characterized in the outer rather than the inner half of the web, and usually included behavior above as well as below the hub (see also Table O6.3 on *M. duodecimspinosa*). One leg was characterized as "following" another if it consistently moved to and grasped a line near to the point where that same line was already held by the other, leading leg, and in which the leading leg then quickly released its hold on the line (typically moving forward to find and grasp another line). "Short-distance searching" movements were the generally small amplitude movements executed by the tip of the leg approximately 0.1s before it grasped a line; they were especially clear when one leg was following another (probably because the approximate location of the line was already known by the spider). They differed from the repetitive, larger-amplitude "long distance searching" leg movements when the spider explored an empty space by waving or tapping with her legs (see text). Legs are indicated by "o" and "i" to indicate their positions during construction: "outer" legs were those directed away from the hub while the spider was spiralling around the web building hub, temporary and sticky spiral lines; "inner" legs were directed toward the hub (e.g., Figs. O6.1 – O6.3). Many of the behavior patterns (both following and short-distance searching) were not absolutely constant, and the characterizations represent the most common types of movements rather than exhaustive lists of all movements. Some species were too small or moved too rapidly (especially *L. mariana*) for me to characterize the movements of certain legs in certain situations. Inconsistent behavior was also not characterized. Thus for instance, some interior legs during sticky spiral construction only occasionally followed others, and were not counted as following. In sum, this table does not provide final characterizations of all leg movements, but rather illustrates two apparently general trends in the more consistent and easily observed types of leg movements: legs often follow the immediately anterior ipsilateral; and short distance searching movements by legs I and II tended to be prolateral in direction, while those by legs III and IV tended to be retrolateral.

Behavioral operation and spider	Following behavior (leading leg – following leg)	*Not* follow any leg	Direction of short-distance searching	
			Prolateral	Retrolateral
Secondary radius construction				
Leucauge mariana TET	I-II; II–I; I–I (contra)[1]	I; II	I; II	-
Micrathena duodecimspinosa AR	I-I[2]	-	-	-
Zosis geniculata UL	oI-iI[2]	-	-	-
Hub construction				
L. mariana TET	oI–oII; oII-oIII; oIII–oIV	oI; iIII[3]	-	oIII[4]; oIV[4]
M. duodecimspinosa AR	oI-oII; oII-oIII; oIII-oIV	oI; iIII[3]	oI; oII; iI; iII	oIII; oIV
Z. geniculata UL	oII-oIV; oIV-oIII[5]	oIII; oII	-	-
Temporary spiral construction				
L. mariana TET	oII–oI; oIII–oII; oIV-oII[6]	-	-	-
Cyrtophora citricola AR[7]	oI-oII; oII-oIII	-	-	-
Nephila clavipes NEP	oII–oIII; oIII–oIV; oI-oII[8]	oI; oII; iI; iII; iIII	oI; oII; iI; iII	oIII; oIV
Zosis geniculata UL	oI-oII; oII-oIII; oIV-oII/oIII[9]	iII; iIII[10]	oI?; oII?	oIV
Sticky spiral construction				
L. mariana TET	oI–oII; oII–oIII; oIII-oIV?[6]	-	-	oIV(?)
M. duodecimspinosa AR	oII-oIII; oIII-oIV	oII	oI;oII	oIII?; oIV[11]
Gasteracantha cancriformis AR	oI-oII[12]; oII-oIII[13]; oII/oIII-oIV[6]	oII[11]	oI[14]; oII[15]	oIII[14]; oIV
Araneus expletus AR	oII-oIII; oIII–oIV; iI–iII; oI– iI	oII, iI	oI(?); oII(?);iI; iII	oIII; oIV
Cyclosa monteverdi AR	oII-oIII; oIII-oIV	iII; iIII	oII -	oIII; oIV; iIII; iIV
N clavipes NE	oIII-oIV[11]	oIII; oII; oI	-	oIII; oIV
Zosis geniculata UL	oI-oII[16]; oII-oIII[13]; oIII-oII[13] oI-iI[17]; iI-oI[17]; iIII-oIII[18]	-	oI; oII[15]	oIII[15]

[1] all three following sequences were common; some other times these legs did not follow each other

[2] as grasp successive possible exit radii

[3] during construction of the first loop did not move at all

[4] the movements were very rapid, so there is some uncertainty in this characterization.

[5] oIV grasped r_n first, then oIII grasped it nearby. But oIV did not then immediately release its grip and move on; instead both legs held the radius as the sticky line was attached between them.

[6] leg oII often left the radius one or two frames of the video recording before oIV arrived; during this time oIII (which had followed oII) remained holding the same radius. The site grasped by oIV was closer to that grasped by oII than to that grasped by oIII. It is thus not entirely clear whether it should be said that oIV followed either oII or oIII.

[7] construction of non-sticky spiral in dense horizontal sheet

[8] behavior occurred while turning from temporary spiral construction to lay a tertiary radius

[9] both oII and oIII were on r_n

[10] at least following was not consistent

[11] the tarsus often appeared to slide (probably making contact on its retrolateral side) along r_n before gripping it

[12] oII followed oI to first seize r_n, but later did not follow oI during inner loop localization behavior when it occasionally grasped r_n briefly while it was tapping to locate the inner loop of sticky spiral

[13] hand-over-hand movements reeling in or walking out r_n, with each leg grasping the radius outside the other; often only 1-2 steps.

[14] when reached to grasp r_{n+1}, but not when tap to locate the inner loop

[15] especially clear as oII and oIII pulled in or walked out r_n hand-over-hand

[16] except on the first sticky spiral on r_n, when oI held the temporary spiral and oII grasped r_n.

[17] infrequent

[18] only the first step of lwg oIII following an attachment

Table O3.1. A sample of orb-weaving species in which the angles between the web plane and horizontal were measured in the field for at least five different adults (data previously unpublished). Specimens were identified by H. W. Levi and B. D. Opell (uloborids). In some cases, in which I spent an extended period in a single site (near Puerto Lopez, Meta, Colombia; near Cali, Colombia; San Antonio de Escazu, Costa Rica; Ayanar Falls, Tamil Nadu, India), I learned to distinguish some species for which I was able to obtain certain identification only to genus; and I have added letters after the genus names to distinguish these species, and give the number of a voucher specimen in the Museum of Comparative Zoology, Cambridge, MA. Some slants were nearly vertical and showed little variation, some were nearly horizontal with also little variation (*Uloborus, Dolichognatha, Enacrosoma*), and others are more intermediate and show substantial variation (*Eustala, Mangora, Leucauge*). I distinguished four somewhat arbitrary categories of web slants: spiders that consistently build nearly perfectly vertical webs (mean > 80^{o}, “strictly vertical”; spiders that also build inclined orbs, but with less steep slopes (about 60-80^{o}) and moderate to high standard deviations (“approximately vertical”; spiders that build somewhat horizontal orbs (20-60^{o}) with moderate to high standard deviations (“approximately horizontal”; and spiders that build close to perfectly horizontal orbs (0-20^{o}) with moderate to small standard deviations (“strictly horizontal”).

Spider	Mean slant ± standard deviation	N	Coefficient of variation
Strictly vertical (>80^{o})			
Alpaida moata (AR)	82.2±7.3	9	0.088
Alpaida septemmammata (AR)	85.1±3.2	8	0.037
Alpaida tuonabo (AR)	80.3±9	7	0.112
Araneus venatrix (AR)	86.3±2.6	7	0.030
Bertrana striolata (AR)	85.4±5	5	0.058
Cyclosa caroli (AR)	83.9±5	23	0.059
Cyclosa tapetifaciens (AR)	82.9±6.4	9	0.077
Cyclosa sp. #2100 (AR)	89.4±1.3	5	0.014
Cyclosa sp. #1978 (AR)	84.2±6.5	13	0.077
Eriophora edax (AR)	84.5±3.8	13	0.044
Eriophora fuliginea (AR)	85.6±5.8	5	0.067
Eriophora ravilla (AR)	82.7±4.2	6	0.050
Eustala fuscovittata (AR)	82.7±9	15	0.108
Gea heptagon (AR)	82.8±7.4	12	0.089
Metazygia benella (AR)	82.8±6.6	5	0.079
Neoscona sp. #2001 (AR)	88±2.5	6	0.028
Ocrepeira sp. #3641 (AR)	83.7±6.2	7	0.074
Pronous tuberculifer (AR)	88.2±1.6	10	0.018
Verrucosa undecimvariolata (AR)	87.8±1.5	5	0.017
Wagneriana acrosomoides (AR)	85.7±3.7	6	0.043
Wagneriana maseta (AR)	85.4±3	8	0.035
Wagneriana tauricornis (AR)	87.7±2.6	10	0.029
Wagneriana undecimtuberculata (AR)	83.6±2.6	18	0.031
Chrysometa sp. #3328 (TET)	81.2±10.6	9	0.131
Approximately vertical (about 60-80^{o})			
Acacesia hamata (AR)	75.5±11.6	14	0.153
Alpaida leucogramma (AR)	69.2±6.4	11	0.092
Alpaida acutas (AR)	76.2±6.8	8	0.089
Alpaida truncata (AR)	74±13	7	0.175

Araneus detrimentosus (AR)	79.4±4.8	5	0.060
Araneus expletus (AR)	78.8±4.3	10	0.054
Araneus veniliae (AR)	59.6±34.5	5	0.578
Araneus sp. nr *legonensis*(?) (AR)	79±8.7	6	0.110
Argiope argentata (AR)	64.3±6.4	19	0.099
Cyclosa insulana (AR)	76.6±10.4	8	0.135
Cyclosa triquetra (AR)	70.3±5.8	7	0.082
Eustala asymmetrica (AR)	67.3±25	6	0.371
Eustala guttata (AR)	75.4±19.4	12	0.257
Gasteracantha cancriformis (AR)	66.9±10	19	0.149
Gasteracantha sp. #1986 (AR)	72.6±8.6	14	0.118
Larinia prob *directa* (AR)	73.8±10.7	6	0.144
Mangora pia (AR)	74.1±7.2	21	0.097
Metazygia gregalis (AR)	71.3±23.1	13	0.323
Metazygia pallidula (AR)	75.8±5.6	5	0.073
Metazygia yobena (AR)	69.1±19.5	7	0.282
Micrathena duodescimspinosa (AR)	74.3±8.7	70	0.117
Micrathena plana (AR)	67±9.2	19	0.137
Micrathena acuta (AR)	62.4±10.8	11	0.173
Micrathena guerini (AR)	75.8±5.7	5	0.075
Micrathena molesta (AR)	69.6±8.8	11	0.126
Micrathena schreibersi (AR)	68.8±7.5	23	0.109
Micrathena sexspinosa (AR)	60.8±11.4	44	0.187
Neoscona nr. *nautica* #1991 (AR)	74.9±13.4	13	0.178
Pronous wixoides (AR)	74.3±8.6	6	0.115
Witica crassicauda (AR)	67.3±23.9	9	0.355
Chrysometa alboguttata (TET)	78.3±8.3	13	0.106
Chrysometa universitaria (TET)	72.4±8.2	5	0.113
Tetragnatha sp. #2043 (TET)	64.1±13.4	12	0.209
Philoponella tingena (UL)	65.3±14	12	0.214
Epeirotypus sp. prob. *chavarria* #2156 (TSM)	79.9±15	12	0.187
Approximately horizontal (20-60º)			
Mangora sp. n. #1641 (AR)	35.8±16.7	12	0.466
Mangora melanocephala (AR)	43.6±16.1	16	0.369
Metazygia lopez (AR)	48.5±26.5	12	0.546
Spilasma duodecimguttata (AR)	30.5±11.4	16	0.373
Leucauge argyra (TET)	27.1±12.9	19	0.476
Leucauge mariana (TET)	31.1±14	36	0.450
Leucauge regnyi (TET)	59±18	200	0.305
Leucauge sp. #1796 (TET)	35.6±16.7	10	0.469

Leucauge sp. #1762 (TET)	47±10.1	7	0.214
Leucauge sp. #1771 (TET)	24±18.5	5	0.770
Leucauge sp. #1779 (TET)	34.2±12.4	6	0.362
Leucauge sp. #2007 (TET)	52.2±14.2	12	0.272
Leucauge sp. #2025 (TET)	46.2±15.3	5	0.331
Tylorida striata (TET)	54.2±6.48	13	0.120
Uloborus trilineatus (UL)	23±12.4	33	0.539
Philoponella vittata (UL)	47±11.1	10	0.236
Philoponella vicina (UL)	52.1±19.2	8	0.368
Zosis geniculata (UL)	52.5±14	11	0.266
Naatlo splendida (TSM)	23.0±15.3	7	0.663
Therdiosoma (?) sp. #1869 (TSM)	58.0±26.6	12	0.459
Strictly horizontal (0-20º)			
Dolichognatha sp. #1503 (TET)	20.8±8.9	13	0.428
Dolichognatha tuberculata (TET)	12.9±9.2	7	0.713
Dolichognatha sp. #1041 (TET)	18.3±11.5	9	0.628
Siratoba referens (UL)	14.8±8.1	15	0.547
Anapisona simoni (AN)	17.3±14.0	24	0.809

Table O3.2. A sampler of orb-weaving species that incorporate detritus or egg sacs into their orbs, and in which other natural history details are known. The list is undoubtedly incomplete, but serves to illustrate the diversity of stabilimentum materials and their sites, and the likely repeated evolutionary convergences. The resting sites, resting positions, and activity cycles of the spiders (all webs were operated during the day) are all in accord with the visual defense hypothesis (Table 3.7); "P" = plant material; "A" = animal remains; "det." = detritus of undetermined provenence); "a" = just above the hub, "b" = just below the hub, "a/b" = both above and below the hub.

Species	Egg sac? (covering)	Type of detritus	Site of stabilimentum	Resting site of spider	Constrained posture?	Web operated in day?	References
Araneidae							
Allocyclosa bifurca	Y (none)	P, A[1]	a/b hub	hub	Y[2,3]	Y	Eberhard 2003, WE
Arachnura spp.	Y	P	a hub	hub	Y[4]	Y	McKeown 1952, Shinkai and Takano 1984, WE (in India)
Cyclosa spp.	Y (P, A)[5]	P, A[5]	a/b hub[5]	hub	Y[2,3]	Y	(many)
Cyrtophora citricola	Y (none)	P	hub (sac) edge sheet (leaf)	hub, sheet	Y[2]	Y	Blanke 1972, WE
Enacrosoma anomala	Y (det.)[6]	P[6]	scattered in horiz. orb	hub	Y	Y	G. Hormiga pers. comm., WE
Tetragnathidae							
Dolichognatha pentagona	Y (P)	P	cylinder hang from frame line[7]	lower tip of stab.[7]	Y	Y	Eberhard 1986*a*, WE
Dolichognatha sp.	Y (P)	P	vertical sheet near hub (Fig. 3.43)	hub[8]	Y[2,8]	Y	WE
Nephilidae							
Nephila spp.	N	P, A	near hub (often in tangle nearby)	hub	N	Y	Robinson and Robinson 1973*a*, 1973*b*, WE
Uloboridae							
Philoponella spp.	Y (none)	none	adjacent to hub	hub	Y[2]	Y	Lubin 1986 (summary)
Philoponella sp. (Parrita, Costa Rica)	Y (none)	none	adjacent to hub		Y[2]		WE
Uloborus glomosus	Y (none)	none	adjacent to hub	hub	Y[2]	Y	Comstock 1967, Cushing and Opell 1990, WE
Uloborus sp. (Australia)	?	det.	scattered in horiz. orb	hub	?	Y	G. Hormiga pers. comm.

[1] the animal detritus included both prey remains and the moulted cuticle (from up to three previous instars) of the spider.

[2] crouched with legs folded tightly against body or in other postions that obscure their leg-like outlines; when frightened spider tenses the sheet with her legs

[3] constrained posture of spider only during the day, not at night

[4] the spider's abdomen also often curled asymmetrically

[5] animal remains were often triturated into small pieces of cuticle; for variants in sites of stabilimenta, see Hingston 1927, 1932

[6] the masses of material (generally smaller pieces of detritus) were similar often more or less spherical, and similar in size to the spider. Each mass dangled from short line attached to a radius in the horizontal orb, and they moved in even light winds in the forest understory.

[7] The stabilimentum was a long cylinder of plant debris that dangled below a frame line line; the horizontal orbs were built near large objects (e.g., tree trunks), and the stabilimentum was at the more sheltered edge. The spider crouched at the lower tip of the stabilimentum (where its outline was difficult to perceive), holding a signal line that ran directly to the hub.

[8] Stabilimentum was a small, vertical curtain of mostly plant debris that hung below one radius near the hub (Fig. 3.43); when disturbed the spider turned and grasped this curtain, thus "wrapping" it around herself

Table O3.3. Types of data that have been used to test the major hypotheses regarding the function of silk stabilimenta (called "stabilimenta" in what follows). Some kinds of data which showed particular trends in some studies but opposite, contradictory trends in others are subdivided in paired entries. The data area grouped loosely by topic, but otherwise the order is arbitrary.

Physical association between spider and stabilmentum

1. Many species that rest on or near the stabilimentum assumed constrained postures during the day that reduced their resemblance to a spider-like outline (eight legs with a central body), and that caused them to merge with the outline of the contiguous stabilimentum (Fig. 3.47). These included numerous species in *Argiope* AR, *Cyclosa* AR and *Uloborus* UL (Hingston 1927, 1932, Wiehle 1927, 1928, 1929, 1931; Marson 1947*a*, 1947*b*). Several species with such constrained day-time postures abandoned them at night, including *Argiope argentata* (Robinson and Robinson 1970*a*, Fig. 3.47), *Allocyclosa bifurca* AR (Eberhard 2003), and *Uloborus diversus* (Eberhard 1973).

2. For all species that build stabilimenta that near or at the hub of an orb (the usual case), the spider rested at the hub, not in a retreat away from the hub. There were no stabilimenta at the hubs of orbs of any of the many species that rested at the edge of daytime orbs (see list of 12 araneid genera in Eberhard 2003; also, summaries in Edmunds 1986; Eberhard 2003, 2008; Blackledge et al. 2011). In the genus *Uloborus* UL nearly all species built stabilimenta and rested at the hub (Marples 1955; Lubin 1986). There were two exceptional *Uloborus* species, in which the spider rested at the edge (*U. gibbosus*) or on a twig projecting through the center of the hub (*U. eberhardi*); both of these species lacked stabilimenta (Marples 1955; WE).

3. Stabilimenta were built by only two species in which the spider rested away from the orb; in both cases, *Araneus legonensis* (Grasshoff and Edmunds 1978) and *Araneus expletus* (Eberhard 2008), the stabilimentum (a sheet of opaque white silk) was placed on the retreat rather than the hub (Fig. 3.49c,d).

4. In some species, nearly all of the many tufts of stabilimentum silk were far from the hub where the spider rested; they were on radii, frame and anchor lines or on a tangle beside the orb. These species included: *Gasteracantha* spp. AR (Fig. 3.48) and its relative *Isoxya* AR (Hingston 1932; Marson 1947*a*, 1947*b*; Peters 1953; Marples 1969; Edmunds 1986; Edmunds and Edmunds 1986); *Thelacantha brevispina* AR (Tseng et al. 2011); *Cyclosa argenteoalba* AR (Takasuka et al. 2015); *Allocylosa bifurca* AR (WE); and *Witica crassicauda* AR (WE, Fig. 3.50).

5. The constrained daytime postures of some species did not cause their outlines to merge with the stabilimentum in several groups. In *Argiope argentata, A. aurantia, A. trifasciata,* and *A. flavipalpis*, the spider's legs were held in an "X" but the stabilimenta were vertical lines (Fig. 3.45, Hingston 1927, 1932; Robinson & Robinson 1970a; Ewer 1972; Eisner and Nowicki 1983; WE). Similarly, in *Philoponella* spp. the spiders crouched at the hub with their legs pressed against their bodies, but neverthless built linear stabilimenta (Opell and Eberhard 1984; Lubin 1986, WE). In *Micrathena* spp. (with one possible exception – see Fig. 3.37a,b) the stabilimentum silk was separated from the spider's outline, and the spider's position was not constrained (Hingston 1932; WE, Fig. 3.37c-j). In *Gasteracantha* spp. (Hingston 1932; Marples 1969) most of the stabilimentum was far from the hub, where the spider rested, and did not merge in any way with the spider's outline, while in *Allocyclosa bifurca* AR occasionally built loose tangles on one side of the orb (always the side on which the spider rested) and these tangles often had sparse, white dots of silk (WE). In *Witica crassicauda* (AR) the spider's abdomen was dark in color, and the stabilimentum was from the hub from the hub where the spider rested (on radii and frame lines), and bore no discernable visual relation to the spider's shape in some populations (though in others it did) (Fig. 3.50) (WE).

Visual impact of stabilimentum and spider

6. All silk stabilimenta were on orbs that spiders operated during the day, despite the large number of species that build nocturnal orbs. The summary of Herberstein et al. cites 78 spp in 22 genera; there have been subsequent discoveries of stabilimenta on diurnal webs of the following: *Molinaria* AR (Levi 2001), *Metepeira* AR (Piel 2001), *M. gressa* (WE), *Araneus expletus* AR (Eberhard 2008), and *Plebs* (= *Eriophora*) *sagana* AR (Nakata 2008).

7. The stabilimenta of many species are highly visible, at least to the human eye (e.g, Hingston 1932; Herberstein et al. 2000b, many others).

8. The spider's color pattern (e.g., stripes on the legs) mimicked the zig-zag pattern of bands of silk in the stabilimentua of *Argiope versicolor* (Seah and Li 2002, *A. argentata* (Schoener and Spiller 1992), *A. bruennichi* (Bush et al. 2008), A. *trifasciata* (WE), and immature *A. aurantia* and *A. savignyi* (Fig. 3.38).

9. The grey, off-white, or silvery white color of the spider mimics the color of stabilimenta in nature in *Zosis geniculata* UL (WE), *Argiope flavipalpis* (Edmunds and Edmunds 1986), *Araneus legonensis* AR (Grasshoff and Edmunds 1978), *Cyclosa ginnaga* AR (Tan et al. 2010).

10. Some morphological traits of species that assumed constrained positions in association with stabilimenta, appear designed to camouflage the spider visually; in *Uloburus* spp. the tuft of setae on leg I obscured the appressed tips of legs II when the spider sat at the hub (Opell 1979; Opell and Eberhard 1984).

11. The vestigial stabilimenta on webs in which a twig passed through the hub were limited to the site where the spider's tarsi II are extended away from the twig to grip hub lines in *Polenecia producta* (Peters 1995; Fig. 3.44).

12. Ontogenetic changes in spider coloration matched changes in stabilimentum traits. Young spiders of *Cyclosa insulana* had a silvery coloration and frequently built white silk platforms; older spiders, in contrast, were darker and usually built dark detritus stabilimenta (Bristowe 1941; Marson 1947*a*, 1947*b*) (see also changes in coloration and the types of detritus and egg sac stabilimenta in *Allocyclosa bifurca* – Eberhard 2003).

13. The stabilimentum silk of *Argiope aurantia* reflects strongly in the blue and green part of the spectrum, making it relatively cryptic to honeybees (and perhaps other insects) in its natural habitat (Blackledge and Wenzel 2000).

14. Some patterns, such as disc and circular stabilimenta, were so dense that they hid the spider from view in *Argiope argentata, A. florida, A. trifasciatus, A. aurantia* and *A. savignyi* (Robinson and Robinson 1970*a*; WE) (Fig. 3.38), and *Lubinella morobensis* UL and *Philoponella* sp. (Lubin 1986).

15a. The size of the space at the center of the hub between different parts of the stabilimentum (e.g. between different arms) was nearly exactly the same as the size of the spider's body, and the spider rested precisely positioned between these parts in *Cyclosa* spp., *Argiope* spp., and *Uloborus* spp. (Hingston 1932; Marson 1947*a*, 1947*b*). **BUT 15b.** In some species the space between the spider's body and the stabilimentum is substantial; the stabilimentum does not blend with the outline of the spider in *Nephila* spp. (Robinson and Robinson 1973*b*), most *Micrathena* (= *Acrosoma*) spp. (Hingston 1932; WE; Fig. 3.37), some *Witica* (Fig. 3.50), or *Gasteracantha* spp. (Hingston 1932; Marples 1969; Shinkai 1969; Murphy and Murphy 2000).

Ontogeny of the spider

16. Stabilimenta appeared during ontogeny in *Gasteracantha cancriformis* AR when webs began to span large distances, and were thus located farther from the substrate where larger animals are more likely to fly (Jaffé et al. 2006).

17. Intermediate-sized individuals of *Argiope argentata* were more likely to have cruciate stabilimenta that increased their apparent size and thus may avoid predation by gape-limited lizard predators that cannot handle large prey[1] (Schoener and Spiller 1992).

18. The form of the stabilimentum varied ontogenetically in *Argiope* spp. (Robinson and Robinson 1970*a*; Edmunds 1986), *A. trifasciata* (Tso 1999), *Gasteracantha cancriformis* AR (Jaffé et al. 2006), and *Uloborus conus* and *Zosis geniculata* (Lubin 1986).

Association between stabilimenta and defensive behavior

19. Some apparent defensive behaviors of spiders when they were disturbed were appropriate to increase the effectiveness of the stabilimenta as visual defenses. Thus *Argiope* spp. with disc stabilimenta shuttled to the opposite side of the hub from a disturbing stimulus, and thus hid behind the disc in *Argiope* spp. (Hingston 1932; Tolbert 1975; Robinson and Robinson 1970*a*; 1974, 1978; Schoener and Spiller 1992; Jackson et al. 1993; Li et al. 2003b). *Cyclosa* spp. AR and *Argiope* spp. also vibrated rapidly or swung the web, blurring the visual images of the spider and the stabilimentum, (Hingston 1932; Robinson and Robinson 1970*a*; Tolbert 1975; Edmunds and Edmunds 1986; Edmunds 1986; Schoener and Spiller 1992; Jackson et al. 1993; Li et al. 2003b) (though apparently defensive webvibration also occurred in species lacking stabilimenta such as *Azilia affinis* TET) (WE). A reduced tendency to vibrate the web was associated with a reduced frequency of stabilimenta (Edmunds and Edmunds 1986). In *A. versicolor*, ontogenetic changes in stabilimentum design and defensive behavior were coordinated, and more shuttling occurred when more disc stabimenta were built (Li et al. 2003b). In addition, both juveniles and adults on webs lacking stabilimenta were less likely to perform their stabilimentum-appropriate defensive behavior than those on decorated webs (Li et al. 2003b)[2].

20. Linear stabilimenta tended to be built on shorter radii that were closer to anchor lines in *Uloborus diversus* UL (Eberhard 1973).

Association between stabiimenta and prey

21. Sticky traps with stabilimenta of *Argiope aurantia* added captured more prey in the field than those without (Tso 1998*a*).

22. Webs in the field with stabilimenta experimentally removed showed less correlation between prey captured and the prey that were "available" in the vicinity in *Argiope keyserlingi* (Bruce et al. 2001).

23. Cruciate stabilimenta are both derived with respect to linear stabilimenta and are more attractive to insects in *Argiope* spp. (Cheng et al. 2010).

24. Stabilmentum construction was induced by the presence of a species of stingless bee[3] in *Argiope argentata* (Craig et al. 2001).

25. More stabilimentum arms (bands) and greater total lengths of their arms were built when prey were supplied more erratically to *Argiope keyserlingi* over time periods of several days, rather than at a constant rate (Herberstein et al. 2000a)[4].

26a. Captive prey (*Drosophila melanogaster* and *Chrysomya varipes* flies, or *Trigona* bees) chose the side of a Y maze or were otherwise attracted to the stabilimenta or UV-reflecting decorations of *Argiope argentata* (Craig and Bernard 1990), *A. keyserlingi* (Bruce et al. 2001), *A. versicolor* (Li 2005; Cheng and Tso 2007), *A. savignyi* (Gálvez 2009), *Uloborus glomosus* (Craig and Bernard 1990), and *Octonobus sybotides* UL (Watanabe 1999b). **BUT 26b.** Stabilimenta did not attract prey in *Argiope keyserlingi* (Bruce and Herberstein 2005) (at least with respect to different stabilimentum patterns) and Rao 2010) or *Gasteracantha cancriformis* (Gawryszewski and Motta 2008).

27a. Webs with stabilimenta in the field captured more prey than those without (*Argiopea argentata* – Craig 1991; Craig et al. 2001; *A. keyserlingi* - Herberstein 2000; *A. trifasciata* – Tso 1996; *A. appensa* – Hauber 1998[5]; *Cyclosa conica* – Tso 1998*b*; *C. ginnaga* – Tan et al. 2010; *Octonoba sybotides*– Watanabe 1999a). **BUT 27b.** Webs with stabilimenta in the field captured fewer prey when differences in site richness were controlled for in *Argiope aurantia* (Blackledge and Wenzel 1999), or captured equal numbers in *A. keyserlingi*[6] (Bruce et al. 2001), *A. argentata* (Craig et al. 2001) and *Gasteracantha cancriformis* (Gawryszewski and Motta 2008).

28a. When either the stabilimentum or both the stabilimentum and the spider were removed, the numbers of prey intercepted by the web *Argiope argentata* declined (Craig and Bernhard 1990). **BUT 28b.** Prey interception, comparing webs with no stabilimenta compared with webs with stabilimenta when prey richness at different sites was taken into account, increased in *Argiope aurantia* (Blackledge and Wenzel 1999), and was not significantly different from control webs with stabilimenta in *Argiope keyserlingi* (Bruce et al. 2001).

29a. The half of an orb with a stabilimentum intercepted more prey than the side without a stabilimentum in *Argiope argentata* (Craig and Bernhard 1990). **BUT 29b.** The half of an orb with a stabilimentum did not intercept more prey than the half without a stabilimentum in *A. trifasciata* (Tso 1996).

30a. Painting the stabilimenta on the tangle beside the orb decreased the numbers of prey striking the orb in one year. **BUT 30b.** The same treatment did not have the same effect a second year, in which the trend (not statistically significant) was in the opposite direction (Tseng et al. 2011).

Association between stabilimenta and predators

31. Wasps in captivity that had available equal numbers of prey spiders (*Argiope trifasciata*) with and without stabilimenta captured more spiders that lacked stabilimenta (Blackledge and Wenzel 2001 on the sphecid wasps *Chalybion caerulium* and *Sceliphron caementarium*).

32. Spiders with stabilimenta on their webs in the field disappeared more often than those without in *Argiope argentata* (Craig et al. 2000), *A. keyserlingi* (Herberstein 2000) and *A. versicolor* (Li 2005).
33. Stabilimenta of juveniles of *Argiope versicolor* in the presence of chemical cues from the salticid spider predator *Portia labiata* differed from those of control spiders in that they were built less frequently, and failed to increase in size over the space of three experimental days (Li and Lee 2004).
34. When a vibrating tuning fork (440 Hz) simulating a predator was held on five occasions close enough to the dorsum of the spider to induce the spider to drop from the hub on a drag line (or, less commonly, to raise its anterior legs), the web built the following day was more likely to have a stabilimentum in *Plebs* (= *Eriophora*) *sagana* AR and *Cyclosa argenteoalba* (Nakata 2008, 2009).
35. Experienced bird predators (*Cyanocilla cristata*) captured *Argiope aurantia* and *A. trifasciata* spiders on webs lacking stabilimenta in preference to spiders on webs with stabilimenta (Horton 1980).
36. Captive butcher birds (*Craticus crassicus*) and blue jays (*Cyanocilla cristata*) responded to contact with orb or tangle lines with intense preening, and learned to avoid the lines of *Nephila clavipes* (Robinson and Robinson 1976) and *Argiope* spp. (Horton 1980).
37. Predators learned to associate prey with artificial stabilimenta resembling those of *Argiope argentata* (Robinson and Robinson 1970*a*), or innately preferred webs with stabilimenta in *A. versicolor* (Seah and Li 2001).
38. Aggregated individuals of the facultatively colonial *Argiope radon*, which may have been more protected from predation (WE), were less likely to build stabilimenta than solitary individuals, and their stabilimenta were shorter (Rao et al. 2009).
39a. Fewer stabilimenta were built in more dense vegetation, which offered increased access for mantid predators in *Argiope keyserlingi* (Bruce et al. 2001). **BUT 39b.** More were built on webs at more exposed sites in *Argiope trifasciata* (Blackledge and Wenzel 2001).
40a. Stabilimenta attracted predators[7] in captivity; mantids were attracted to *Argiope keyserlingi* (Bruce et al. 2001) and salticid spiders were attracted to *A. versicolor* (Seah and Li 2001; Li and Lim 2005). **BUT 40b.** Stabilimenta repelled a potential predators in the field in *Argiope argentata* (Robinson and Robinson 1970*a*), and in captivity stabilimenta of *Argiope aurantia* and *A. trifasciata* had a repellent effect on experienced birds, and no attractant effect on naïve birds (Horton 1980).
41a. Sphecid wasps had in their nests paralyzed individuals of spider species of *Argiope, Cyclosa, Gasteracantha* that build stabilimenta–Elgar and Jebb 1999 on the wasp *Sceliphron laetum*,WE on the wasp *S. caementarium*). **BUT 41b.** Some nest contents showed an apparent bias against capturing *Argiope* spiders with stabilimenta (Adato-Barrion 1981 and Edmunds 1986 on the wasps *Chalybion fuscipenne* and *S. spirifex*).

Association between stabilimenta and large animals that might damage webs

42. The webs of some species that build stabilimenta generally occur in very sheltered sites, such as deep in tall grass, deep in piles of sticks, and between stilt buttress roots, where large, fast-moving visually orienting animals probably seldom go. This is true for *Argiope* spp. (Edmunds 1986; Edmunds and Edmunds 1986; Seah and Li 2002; Li et al. 2003a; WE), *Conifaber parvus* (Lubin et al. 1982), *Philoponella vicina* (WE), *Uloborus diversus* (Eberhard 1973), *Lubinella morobensis* UL (Lubin 1986), and other species of *Uloborus* and *Philoponella* (Lubin 1986).
43. Populations on islands that lacked predators showed fewer stabilimenta in *Argiope argentata* (Lubin 1975), and *A. appensa* (Kerr 1993)[8].
44. Birds were substantially less likely to damage a web placed near a dish of bird seed on a mown lawn when the web had a stabilimentum in *Argiope aurantia* (Blackledge and Wenzel 1999).
45a. Webs with stabilimenta were less often destroyed during the day in *Argiope florida*[9] (Eisner and Nowicki 1983) and *A. aurantia* (Blackledge and Wenzel 1999), and experimental web damage resulted in increased investment in stabilimenta by *A. keyserlingi* (Walter and Elgar 2011). **BUT 45b.** Painting stabilimenta black (and thus presumably reducing their visibility) had no effect on web damage in *Gasteracantha cancriformis* (Gawryszewski and Motta 2008).

Mechanical properties of stabilimenta

46. The silk fibers of stabilimenta were generally very loose, rather than tense, and they were often attached to the web in ways that would not strengthen it; these included masses of loose lines that were attached to a single web line in *Uloborus diversus* UL, *Gasteracantha* spp. AR, and *Argiope* spp. AR (Eberhard 1973; Edmunds 1986; Herberstein et al. 2000b), or to a single line or lines below the orb in *Philoponella herediae* UL (Opell 1987) and *Uloborus diversus* UL (Eberhard 1973).
47. Stabilimenta were almost never limited to (and generally did not even extend substantially into) the capture area of the orb (sticky spiral). They were thus inappropriately placed to function to capture drawn to them in many species (e.g., Hingston 1932; Herberstein et al. 2000b). Some *Micrathena* spp. (AR) are an exception (Hingston 1932 on *Acrosoma*, C. Craig unpub cited by Herberstein et al. 2000b).
48. Circular stabilimenta increased tensions on radii, and thus increased the spider's ability to capture small prey in *Octonoba sybotides* (Watanabe 2000).
49a. More stabilimenta were built on windy days by *Cyclosa insulana* (Neet 1990) **BUT 49b.** No more stabilimenta were built at windy sites than at non-windy sites in the field by *Argiope argentata* (Lubin 1975; Nentwig and Rogg 1988), and fewer were built in captivity by *Uloborus diversus* subjected to a gentle wind (Eberhard 1973).

Contexts of individual and intra-specific variation in stabilimenta

50. Stabilimenta occurred on resting or moulting webs, which include few or (usually) no sticky lines and are thus not designed to capture prey. Stabilimenta were found on resting webs in *Gasteracantha* spp. (Edmunds 1986); *G. versicolor* (Emerit 1968); *G. cancriformis* (Marples 1969; Jaffé et al. 2006); *Allocyclosa bifurca* (WE); *Nephila clavipes* NE (Robinson and Robinson 1973*b*, 1976, Fig. 3.48), *N. maculata* (Shinkai 1985), *Trichonephila* (= *Nephila*) *inaurata* (Kuntner et al. 2008a), *Uloborus filinodatus* UL (Hingston 1932), *U. globosus* (WE), *U.* sp. (WE), *Philoponella vicina* UL (WE), *Zosis geniculata* and *Z.* sp. UL (both the resting webs of mature males (Figs. 3.48, 9.21) and occasional hubs without any sticky spiral lines built by mature females near egg sacs) (Fig. 10.35), *Cyclosa conica* AR (Tilquin 1942), *Allocyclosa bifurca* AR (WE), *Argiope bruennichi* AR (Marples 1935; Tilquin 1942), *A. keyserlingi* (Walter et al. 2008), *A. aemula* (Robinson and Robinson 1978), *A. argentata* (Robinson and Robinson 1970*a*, 1978; Nentwig and Rogg 1988), and *A. flavipalpis* (Ewer 1972; Edmunds 1986) (because of the importance of these observations, I have given separate citations for different species). In *N. clavipes* (Robinson and Robinson 1973*b*, *A. argentata* (WE) the frequency of stabilimenta was greater on resting webs than on prey capture webs Robinson and Robinson 1976; Nentwig and Rogg 1988. In *N. clavipes* (Robinson and Robinson 1973*b*, WE), *A. bruennichi* (Tilquin 1942) and *A. argentata* (WE) some spiders molted on a resting web with a stabilimentum (WE). In *A. argentata* (Robinson and Robinson 1970*a*), *A. flavipalpis* (Edmunds 1986), *G. cancriformis,* and *Z. geniculata* (WE) the stabilimenta on resting webs appeared to be larger and denser than those on normal prey capture webs, though no quantitative measures were made of the amounts of silk. In *A. versicolor* (Murphy and Murphy 2000) and *Z. geniculata* (WE) the resting webs of mature males, which also lacked sticky spiral lines, had stabilimenta.

51. Stabilimentum patterns varied substantially from day to day in same individual in *Argiope* spp. (Ewer 1972; Edmunds 1986; Craig 1994*b*), *Uloborus diversus* and *Zosis geniculata* (WE), and several other uloborids (Lubin 1986); they also varied in the same population of *Argiope* spp. (Ewer 1972; Edmunds 1986), *Uloborus diversus* (Eberhard 1973) and *Allocyclosa bifurca* AR (Eberhard 2003); and between populations of the same species *Argiope flavipalpus* (Edmunds 1986).

52. Depletion of aciniform gland contents in *Argiope aetheroides* reduces the sizes of stabilimenta, and thus invalidates conclusions from variation because the variation is due to recent feeding history (Tso 2004).

53. Better-fed spiders were more likely to produce more or larger stabilimenta in *Argiope aurantia* (Blackledge 1998a), *A. trifasciata* (Tso 1999)[10], *A. argentata* (Craig et al. 2001), and *A. keyserlingi* (Herberstein et al. 2000a).

54. Better fed individuals of *Octonoba sybotides* were more likely to build linear rather than circular stabilimenta (Watanabe 1999a).

55. Lower temperature weather (when prey may have been more scarce) correlated with more stabilimenta in *Argiope keyserlingi* (Herberstein and Fleisch 2003).

56. Stabilimentum construction was induced by removal of eggs sacs that camouflage the spider, and inhibited by addition of egg sacs in *Allocyclosa bifurca* AR (Eberhard 2003). In *Cyclosa fililineata* and *C. morrretes* AR (Gonzaga & Vasconcellos-Neto in press) stabilimentum construction was induced by destruction of the entire web, but the reciprocal experiment to see if silk stabilimentum construction was suppressed when detritus was added was not performed. Marson (1947*b*) observed that detritus was later included following destruction of the webs of *C. insulana.*

57a. More stabilimenta were built when the light level during the night was brighter in *Argiope pulchella* (Marson 1947*a*) and *Uloborus diversus* (Eberhard 1973). **BUT 57b.** Fewer and or smaller stabilimenta were built at brighter sites in *Argiope versicolor* (Seah and Li 2002), *A. keyserlingi* (Bruce et al. 2001[11]; Herberstein and Fleisch 2003), or when *Argiope aetherea* spiders were in frames covered with white as opposed to black mosquito netting (Elgar et al. 1996). In addition, there was no difference when illumination differed in *Argiope flavipalpis* (Edmunds 1986), *A. keyserlingi* (Rao et al. 2007), or in *A. argentata* (Nentwig and Rogg 1988).

58. Food-deprived spiders reduced the sizes and numbers of stabilimenta in *Argiope aurantia* and *A. trifasciata* (Blackledge 1998a).

Et cetera

59. Spiders appeared to drink water from stabilimentum silk lines at the hub but not elsewhere when the orb was sprayed with water in *Argiope bruennichi* AR (Walter et al. 2009).

60. Stabilimentum arms below the hub were longer than those above it in *Argiope aemula, A. picta, A. reinwardti* (Robinson and Robinson 1974), *A. trifasciata* (Tso 1996), and *Nephila clavipes* NE (Robinson and Robinson 1973*b*).

[1] For a similar argument based on size limits of predators in relation to the defensive properties of barrier webs in *Argiope*, see Tolbert (1975).

[2] Smaller individuals of *A. appensa* were not more likely to shuttle, however (Jackson et al. 1993).

[3] The experimental manipulation was the mowing down of nearby flowering grasses. One effect (among many other possibilities) was to reduce the density of bees. There is reason to suppose that the mowing also reduced the aerial populations of many other prey insects (Chacón and Eberhard 1980); thus the possibility that reduced stabilimentum production was simply due to poorer overall feeding success rather than absence of this species of bee cannot be discarded.

[4] Assuming that the densities of the silk in the arms was constant (not tested), then spiders that were fed erratically invested more heavily in stabilimenta.

[5] Decorated orbs were smaller, but caught more prey/cm^2. Classification of this study as showing more prey trapped/cm^2 in decorated webs (as argued by the author) is uncertain, because use of an alternative prey counting technique gave results that contradicted the prey attraction hypothesis (footnote 3 in Table O3.5).

[6] In an especially well-controlled experiment with *A. keyserlingi*, there was no significant difference in the numbers of prey between webs with and without stabilimenta (Bruce et al. 2001). There was, however, a significant interaction between "available" prey (which were estimated from catches in an artificial adhesive trap near the web) and stabilimentum presence; given the multiple problems associated with attempts to estimate "available" prey with such traps (Eberhard 1990*b*), I have not followed the authors' interpretation, and have counted this study as *not* showing a positive effect of stabilimenta on prey capture (see also Table O3.5).

[7] These predator species were the only predators observed to eat spiders in the field; but the fact that they consume the spider gradually, at or near the capture site, could make their predation easier to observe than that of other possible predators such as sphecid wasps, birds and lizards, which leave the site immediately. Thus their relative importance in the field is uncertain.

[8] It was not specified whether or not the extinct birds were potential spider predators.

[9] The species was not specified, and a second species of *Argiope* (*A. aurantia*) was also present at the site. The model stabilimenta used were apparently similar to those of *A. florida*, not those of *A. aurantia*.

[10] Spiders fed in captivity greatly increased stabilimentum production, but those in the field (each was surrounded by a nylon screen cage) showed no response to feeding.

[11] The difference reported was vegetation density. It is not certain whether this was associated with the darkness of the site.

Table O3.4. A critical (and unavoidably somewhat subjective) summary of the implications of the evidence in Table O3.3 for the four major hypotheses for stabilimentum (stab) function. The implications are categorized to indicate data that favor a hypothesis (F), argue against a hypothesis (A), or that are equivocal (have no necessary relation to the hypothesis) (-). There are so many types of data, and they pull in so many different directions that I have attempted to provide further orientation by recognizing sub-categories with respect to the strength of the implications for each hypothesis. Some of these classifications are only tentative, and another person would almost certainly change some of them. For instance, the line between data that are unrelated to a hypothesis (-) and that show a trend that is not predicted by a hypothesis (A_4) is difficult, and some data in category A_4 could be converted to category $-_1$ by modifying or extending the hypothesis in a way that did not occur to me. Some correlations (especially those with few data) may change with future discoveries. The implications given for the different hypotheses are mine, not necessarily those of the author, and justifications for many of the categorizations are given in the footnotes. I have tried to take into account the multiple kinds of serious short comings that are common in direct experimental tests of stabilimentum function. The severity of these short comings obviously varies between different studies. I have also tried to be strict rather than lenient in pointing out possible shortcomings. As argued by Popper (1972), the most important advances in science come from strong rejections of hypotheses (categories A_1 and A_2) (for an opposite view, see Starks 2002). I have resisted the temptation to sum up the numbers of different types of implications for each hypothesis, because these data truly represent apples and oranges (and large and small apples and oranges at that). Despite all of these limitations, one important conclusion is clear: all of the hypotheses have some data that argue strongly against them (the most powerful data for and against each hypothesis are indicated in bold).

Favor the hypothesis (F):

F_1 Strong support, because the data demonstrate an observation or trend that is a logical necessity of the hypothesis; a lack of the trend would have been grounds for rejecting the hypothesis

F_2 Moderate support, because the data demonstrate an observation or trend that is predicted by the hypothesis; its lack would not have been sufficient to reject the hypothesis

F_3 Weak support; the trend in the data can be argued to fit the hypothesis, but was not necessarily predicted (and, in some cases, the trend was not convincingly demonstrated in the study species or clearly does not occur in other species).

Against the hypothesis (A):

A_1 Very strong rejection, because the data demonstrate an observation or trend that is opposite to that predicted by the hypothesis; they are grounds for rejecting the hypothesis.

A_2 Strong rejection, because the data demonstrate that an observation or trend that is a logical necessity of the hypothesis do not occur; they are grounds for rejecting the hypothesis.

A_3 Moderate rejection, because the data demonstrate the lack of an observation or trend that was predicted by the hypothesis; they argue against the hypothesis but are not sufficient to reject it.

A_4 Weak rejection, because the data are weak, or demonstrate an observation or a trend that was not predicted by the hypothesis but they do not contradict it; they argue against the hypothesis but are not sufficient to reject it.

Equivocal (-):

- No conclusion merited, because the data have no obvious logical relation with the hypothesis, because the trend or observation is not predicted by the hypothesis but is not incompatible with it, or because the hypothesis can be reasonably modified or extended so that the data are predicted by it.

	Hypothesis			
Evidence	Stabilize web	Attract prey	Warn animals	Visual defense
Physical association between spider and stabilimentum				
1 Cryptic daytime posture (only) that "fits" stab	**A_2**[1]	-[2]	A_3	F_2
2 Stab at hub when spider at hub	F_2[3]	**A_2**	A_3	**F_1**
3 Stab on retreat (not hub) when spider in retreat	**A_2**[4]	**A_2**	A_1	F_2
4 Stab far from spider in web	-	-	-	**A_1**
5 Many stabs far from spider, not merge outlines	-	-	-	**A_2**[5]
Visual impact of stabilimentum and spider				
6 Stabs only on daytime webs	A_3	**F_1**	**F_1**	**F_1**
7 Stab silk highly visible (humans)[6]	-	**F_1**	**F_1**	**F_1**[7]
8 Spider markings mimic stab pattern[8]	A_4	-[2]	A_4	F_3
9 Grey color spider similar to stab[8]	A_4	-[2]	A_4	F_3
10 Other morphological traits for camouflage	-	-	-	F_3
11 Reduced *Polenecia* stab perfect camouflage[9]	A_3	A_3	A_3[10]	F_2
12 Ontogenetic changes in body color match those of stabs	A_4	A_4	A_4	F_3
13 Stab silk less visible to insects vs vertebrates[11]	-	A_4	-	-
14 disc stabs hide spider	-	-	-	F_2
15a Space between stab arms fits spider exactly	A_4	A_4[12]	A_4	F_2[13]

15b Space not fit spider’s body	-	-	-	A_3[13]
Ontogeny of spider				
16 Stabs associated with webs with large spans	-	-	F_2	-
17 Intermed size spiders make design appropriate against gape-limited lizards	A_3	A_3	A_3	F_3
18 Ontogenetic variation stab designs	F_3	F_3	F_3	F_3
Association between stabilimentum and defensive behavior				
19 Defensive behavior of spider is appropriate to enhance visual defense by stab[14]	F_3[15]	A_4[16]	-	F_2
20 Stabs on shorter radii near anchor lines[17]	A_4	A_4	A_4	A_4
Association between stabilimentum and prey				
21 Sticky trap with stab captures more prey	A_4	F_2[18,19]	A_4	A_4
22 Less correl. with available prey if lack stab[20]	-	-	-	-
23 Cruciate stab derived and more attractive[21]	-	F_3	-	-
24 Stab production induced by stingless bees	A_4	F_3[22]	A_4	A_4
25 More erratic capture rates, more stabs	A_4[23]	?	A_4	A_4
26a Captive prey choose stab in Y maze	-	F_3[24,25]	-	-
26b Captive prey not attracted to stab	-	A_3	-	-
27a Field webs with stabs captured more prey[26]	A_4	F_2[26]	-	-
27b Field webs with stabs captured fewer prey[26]	A_4	**A_2**	A_4	-
28a Removal stab decreased prey interception	A_4	**F_1**	A_4	A_4
28b Removal stab increased prey interception	-	**A_1**	-	-
29a Half of orb with stab captures more prey	A_4	F_3[18,27]	A_4	A_4
29b Half of orb with stab not capture more prey	-	**A_1**[27]	-	-
30a Paint stab black reduced prey	-	F_2	-	-
30b Paint stab black not reduce prey	-	A_4	-	-
Association between stabilimentum and predators				
31 Captive spiders with stabs captured less by predator	-	-	-	F_3[28]
32 Spiders in field with stabs suffer greater mortality[29]	-	-	-	A_3[30]
33 Chemical cue of predator inhibits stab const.[30]	A_3	A_3	F_3	**A_2**
34 Sound of predator induces stab const.	A_4	A_4	A_4	F_3[31]
35 Experienced birds pref. spiders w.o. stab	-	-	F_3	F_3
36 Birds bothered by contact with silk	-	-	F_2	-
37 Predators can learn to use stabs to find prey	-	-	-	F_3[30]
38 Coloniality affects learning[33]	A_4	-	F_3	F_3
39 More stabs if webs more exposed (or less dense vegetation)	F_3	-	F_3	-[34]
40a Stabs attract predators in captivity	A_4	A_4[18,35]	A_4	A_4,[36,37]
40b Stabs repel predators in captivity	A_4	A_4	A_4	F_3
41a Wasps capture spiders w stabs (field)[38]	A_4	A_4	A_4	A_4
41b Wasps capt. fewer spiders w stabs (field)[38]	A_4	A_4	A_4	F_3
Association between stabilimenta and large animals that might damage webs				
42 Stabs on webs in sheltered sites	-	-	**A_2**	-
43 Fewer stabs on islands lacking bird pred.[39]	A_4	A_4	F_2	F_3
44 Birds avoid stabs at bird feeder	-	-	(F_2)[40]	-
45a Presence model stab reduced web damage	A_4	A_4	F_3[41]	A_4
45b Paint stab black not increase damage	A_4	A_4	A_3[41]	A_4
45a. Web damage elicits more stabilimentum	A_4	A_4	F_2	A_4
Mechanical properties of stabilimenta				
46 Silk fibers in stab are lax, cannot absorb strain	**A_2**	-	-	-
47 Stabs not placed amidst capture lines	-	A_3[42]	-	-
48 Circular stab lines tense radii[43]	-	-	-	-
49a Stabs are correl. with wind	F_2[44]	-	-	-
49b Stabs are not correl with wind	A_4	-	-	-
Contexts of individual and intra-specific variation in stabilimenta				
50 Stabs are built on webs that are incapable of capturing prey	-[45]	**A_1**[46]	-	-
51 Intra-specific variation reduces learning	-	-	A_3[47]	F_3[48]
52 Smaller stabs when deplete aciniform gland[49]	-	-	-	-
53 Smaller stabs when recently fed less[50]	-	**A_2**[51]	-	-

54 More linear stabs if better fed	F_3[52]	-	-	-
55 Disc stabs hide spider from view	-	-	-	F_2
56 Lack of camouflage material induces construction of stabs	A_3[53]	A_3[54]	A_4	F_3
57a More stab built if light brighter[55]	A_3	-	-	-
57b More stab built if light dimmer[55]	-	-	-	-
57c No effect of lighting on stab production[55]	-	-	-	-
58 Less food, fewer stabs	-	-	-	-
Et cetera				
59 Spider drinks from stab[56]	-	-	-	-
60 Stabilimentum larger below than above hub[57]	-	-	A_3	A_4

---

[1] The sample size is large, so although the hypothesis does not generate a specific prediction, its predicted lack of a trend is contradicted strongly by the data.

[2] If prey attraction hypothesis is modified to include hiding spider from prey (see text), then this observation is predicted by the hypothesis.

[3] If one assumes the spider's own weight at the hub imposes an increased need for stabilization of the web.

[4] Retreat is mechanically very stable compared with the orb, and thus presumably needs no mechanical reinforcement (and the lines in the stabilimentum are not taut).

[5] The constrained posture of the spider argues for attempted visual defense; this could increase the effectiveness of the "distraction" version of the visual defense function, possibly reducing the strength of the conflict with the visual defense hypothesis.

[6] This clearly the general case, but there are exceptions of relatively inconspicuous stabilimenta, as in *Philoponella vicina*, some *Micrathena* species (WE) In any case, as noted by Hingston (1932) with respect to detritus stabilimenta in *C. confusa*, drawing a potential predator's attention is not necessarily equivalent to increasing the overall danger from that predator, if its attacks are misdirected or it is unable to recognize spider as a potential food item (see discussion of the "distraction" function in Table 3.7).

[7] Visibility per se does not argue against visual defense. If highly visible stabilimenta obscure or distort the spider's outline enough that predators do not learn to associate them with the presence of the spider prey, they can function as camouflage (Edmunds 1986; Eberhard 2003).

[8] In nearly all cases the colors and patterns were those perceived by humans; the possibility that inclusion of UV would have changed these evaluations was not tested. This weakens the conclusions.

[9] The precise fit with the visual defense hypothesis is so difficult to explain with any of the other hypotheses that the strengths of both confirmations and rejections are strong for this species.

[10] The modified version of the prey attraction hypothesis that includes visual camouflage is not able to explain this case, because of the complete absence of stabilimentum silk except in the small patch that hides the spider's tarsi.

[11] Only one (non-native) insect species was tested. In any case, measuring an organism's sensitivity to a given wavelength can yield information on the distance at which the stimulus can be perceived; but it is not sufficient to determine the animal's preference for such a stimulus (see discussion of UV in the text). This weakens the conclusions regarding stabilmentum function.

[12] Becomes F_3 if the attraction hypothesis is modified to include visual camouflage.

[13] The distraction function of visual defense could operate even if the outlines of the stabilimentum and the spider are separate. I believe, however (*contra* Hingston 1932), that this argument cannot be reasonably extended to stabilimenta like those of *Gasteracantha* spp.

[14] The stimuli used to elicit defensive reactions (taps on the spider's body with a brush or with other objects like a pencil eraser) or on hub, frame or radial lines, or sudden, localized puffs of air) were thought to simulate stimuli perceived by spiders in situations of risk in nature. Although these suppositions seem reasonable, at least as a first approximation, the stimuli that spiders perceive and respond to when attacked by different predators have not been established experimentally.

[15] The mechanical function hypothesis could be supported if the stabilimentum function is to reinforce the hub to make it more difficult for a predator to penetrate from the opposite side (Li et al. 2003a,b).

[16] Modification of the prey attraction hypothesis to include visual defense is not reasonable in this case. It does not seem likely that by swinging herself energetically on her web the spider reduced her visibility for a prey and induced it to approach her web more closely.

[17] As noted by Watanabe (2000), this trend in stabilimentum oriention is compatible with additional hypotheses, in addition to the visual defense hypothesis that was originally mentioned (Eberhard 1973). Facilitating the spider's escape from the web by orienting the stabilimentum's orientation is potententially independent of the function of the stabilimentum itself.

[18] The multiple differences between a sticky trap and an orb in visibility, visual background (Craig 2003), siting, air flow, and their poor ability to mimic orb captures under unusually favorable conditions (Castillo and Eberhard 1983) all make the relevance of these data to understanding natural orbs highly uncertain (Eberhard 1990*b*). The constrast in the results of a similar experiment using the orbs of this same species (Blackledge and Wenzel 1999) (fewer prey in webs with stabilimenta) gives further reason for doubt.

[19] Prey were counted but not weighed (or only small *Drosophila* prey were used in experiments); because the biologically important payoff to spiders is prey mass rather than numbers (Venner and Casas 2005; Blackledge 2011) and attractiveness may vary for different prey (Tso 1999), this measure of web effectiveness is not entirely convincing.

[20] I am unable to understand the authors' claim of support for the prey attraction hypothesis. I see no reason under any of the hypotheses to expect a match between the bias in the sample of the "available" prey (a seriously unreliable indicator of the prey actually available to spiders – see Eberhard 1990*b*, section O3.2.3); in addition, prey were quantified inappropriately by number rather than nutritional value.

[21] But linear stabilimenta were derived at least three times in the preferred phylogeny (Cheng et al. 2010) (accepting the typological characterization of each species – caution is suggested by the intra-specific variation in the adults of some (Hingston 1932; Herberstein et al.

2000b) and the immatures vs. adults in *A. argentata* (Robinson and Robinson 1978) and *A. florida* (Justice et al. 2005). In addition, species with cruciate stabilmenta often build incomplete crosses with only one or two arms (e.g., Hingston 1932; Herberstein et al. 2000b). In addition, the measure of attractiveness (the number of insects entering the field of view of a camera – apparently mostly Diptera) did not distinguish prey size (and probable nutritional importance) or identity. This is important because the presumed attractiveness of cruciate patterns may well not be true (of 8 references cited to document this preference, five concerned bees, two "pollinators", and the other concerned models rather than data). There are, of course, many insects that fly which are not pollinators. In sum the correlation does not provide convincing evidence regarding any of the hypotheses.

[22] This hypothesis is favored only if stabilimenta are specialized to attract stingless bees. The wide range of *A. argentata* (from USA to Chile) includes areas in which stingless bees are rare or absent, making this hypothesis seem unlikely. In addition, the claims about the importance of the stingless bee, *Trigona fuscipennis*, in the spider's diet, are inconsistent ("one of its most important prey" on p. 987, the "most important prey" on p. 989, and are not supported by the extensive data on the prey of this species (collected previously at exactly the same site). Robinson and Robinson (1970*b*) found that during the 4-5 month dry season (when trees in the canapy were flowering) that these bees were entirely absent. Throughout the year, bees (all species grouped) comprised only an estimated 17% of the diet by weight.

[23] Predictions given by the authors regarding the effects of the erratic rather than uniform rate of prey capture on foraging investments were highly speculative and possibly contradictory, so the conclusions to be drawn from the pattern in the data are not certain.

[24] In some experiments the prey behavior may be an artifact of captive situation, as insects may have been trying to escape (exhibiting an "open space response" – Craig 2003). In others where this was not a problem (e.g. those with foraging stingless bees) only certain limited combinations of behavioral contexts (flight very near the entrance to the hive) and of lighting and visual background were used that may not have been representative of the conditions in nature under which bees usually encounter orbs (far from the hive). In addition, there is no evidence that the responses of the single insect species in each study are representative of the large array of prey captured in the field, nor that these particular species were especially important components of the diets of these spiders (especially in terms of their weight). This evidence (on both sides) is thus weak.

[25] The conclusions are weakened by lack of ecological realism in the setting in which observations were made (e.g., illumination, visual background, behavioral distractions, hunger level). In addition, the conclusions are weakened by lack of knowledge of the relative effects on different groups of predators or prey on the spider in the field. The intensity of natural selection on the spider's reproduction exercised by particular species of predator or pre
is likely to differ under natural conditions.

[26] See Table O3.5 for detailed examination of the data and their implications.

[27] There are serious doubts regarding this technique (see text).

[28] In this highly unnatural situation (wasp enclosed in a small space with spiders), wasps may not have used the same cues to locate prey as in the field, where they may not encounter prey until after first sensing preliminary, long-range cues.

[29] The studies could not distinguish death by predation from long distance emigration, so the conclusions regarding predation rates are weakened (Higgins 1992 emphasizes the importance of making this distinction; for an example of how difficult it is to actually distinguish mortality from movement to a new site see Lubin et al. 1993). In the *A. versicolor* study, 5 of 12 supposed mortality events were confirmed to be due to predation by a salticid spider. A similar study of the effects of detritus stabilimenta in *Nephila edulis* and *N. plumipes* (which suffered from the same shortcoming of attributing all disappearances to predation) suggested a different effect: there was no influence on rates of disappearance (Griffiths et al. 2003).

[30] the stabilimenta built by juvenile *Argiope versicolor* in this experiment were dense arrays of white zig-zag ("disc") lines at the hub. This stabilimentum design is more widely thought to have a direct visual shield effect, even by proponents of alternative functions for other stabilimentum designs (Robinson and Robinson 1973*b*, 1974), and is also associated with defensive behavior appropriate to defense but not prey attraction (Table O3.3), making this contradiction of the visual defense hypothesis prediction particularly striking. There are several further considerations. It was not certain whether the concentration of predator odor was ecologically realistic, however; it would seem likely to be much higher in the enclosed cages than in nature. The relative importance of this predator vs. others, and thus of the costs of stabilimentum reduction in predation and prey capture were not determined. Also puzzling is the fact that the differences measured in stabilmentum area (and also in the capture area and the sticky spiral length) were not due to reductions in experimental webs exposed to *Portia* odor, but rather to sharp, approximately 50% increases in the controls. The reason for these increases was not clear. One related species, *A. appensa*, did not respond to predator odors in a different context (Jackson et al. 1993). Taken together, these considerations introduce some doubt regarding the strength of the conclusions which can drawn.

[31] The logic of this conclusion is based on the questionable and untested assumption that in nature the sound of nearby predators on one day is correlated with the likelihood of attack by a predator on the following day.

[32] The question is not whether predators are *capable* of learing to associate stabilimenta with food (as demonstrated in the *A. argentata* study), but whether they *do* learn this association in the wild. At the beginning of the *A. argentata* experiment, the wild birds *avoided* stabilimenta, demonstrating that they had not learned this association. This study favors the visual defense hypothesis (weakly, because of the small sample) rather than contradicting it.

[33] This correlation involves only a single species, and did not differentiate cause and effect, thus weakening conclusions that can be drawn.

[34] Greater density of vegetation could promote easier access for a mantid predator (Bruce et al. 2001); but it could also hinder predation by other species, such as birds. Without information on the relative importance of different predators, the implications of these data are not clear.

[35] The observation may be an artifact of captivity. The experimental chambers were relatively small and featureless. The predator or prey may have been attempting to escape, and thus attracted by stimuli that are not usually attractive under more natural conditions.

[36] The relative importance of these predators compared with others under natural conditions was not documented. The relative importance of the mantid i
the field, compared with for instance that of birds, lizards, and wasps is difficult to determine because predatory events by mantids, which remain near the web consuming the spider, are much more likely to be observed than those by other types of predators which would immediately carry the spider away.

[37] This may be an artifact of captivity, as the predator may have been attempting to escape. This objection is weaker in the mantid study because all trials that were counted ended with the mantid reaching for the spider (apparently in a predatory attempt) (Bruce et al. 2001). The mantids were naïve, with no previous experience with stabilimenta. This mantid is only one of several possible predators, however, weaking the conclusions.

[38] Neither the bias for nor the bias against predation on spiders with stabilimenta is conclusive because no data are available regarding possible biases in other aspects of the wasps' searching behavior. For instance, under-representation of a species with stabilimenta might be due to a bias against searching i the habitats where this species occurred, or a bias against particular cues associated with the sub-habitat in which spiders occurred; similarly, capture of species with stabilimenta could occur because of a strong bias to search in appropriate sites, despite partial protection conferred by the stabilimenta. Biases determined on the basis of data using human searching capacities are not relevant.

[39] Lack of birds could mean both that visual predators were less common (reducing the need for visual defense), and that there were fewer large animals that broke webs accidentally (reducing the need for warning). The short time since the extermination of the birds in the *A. appensa* study makes conclusions tentative (but both the differences and the sample sizes were large).

[40] The prediction is weak, due to the un-natural situation of large frames containing spider webs placed on an open lawn near bird food (Herberstein et al. 2000b).

[41] Neither the data for or against are generally convincing. The context of the observations of avoidance by birds near a bird bath (*A. aurantia*) is so different from that of foraging that it is difficult to draw ecologically realistic conclusions (see also Herberstein et al. 2000b). In the *A. florida* study, the use of models, which had undetermined degrees of resemblance to stabilimenta in the eyes of birds, rather than real stabilimenta, introduces uncertainty. The sample size in this study is too small to justify confident conclusions. On the other hand, the relatively lower visibility of blackened stabilimenta was determined only for human vision; it could also vary with lighting and background (see Fig. 3.45).

[42] The stabilimentum lines below the orb in *Philoponella* could deter predation by providing a visual distraction to predators (Opell 1987) or by advertisin the presence of a barrier web (visual defense hypothesis). The strength of the rejection depends on the directness of the supposed flight of insects if they ar attracted toward the stabilimentum and the angle from which they approach. The more direct the flight path and the more nearly perpendicular to the web plane, the more convincing this rejection will be. If prey veer away from the stabilimentum at close range after being attracted from a distance, as propose by Rao (2010) to explain a lack of attraction from a distance (I know of no direct observations of this detail), the rejection would be weakened.

[43] The reasons to doubt a cause-effect relationship between circular stabilimenta and radial tensions (see footnote b in

[44] Data are weak for several reasons (see Herberstein et al. 2000b). Increased loss of detritus stabilimenta in storms could have produced the same increase in silk stabilimenta that was observed: production of silk stabilimenta is experimentally increased in other *Cyclosa* species by lack of detritus (Gonzaga &Vasconcellos-Neto in press).

[45] Even though the resting webs are more stable than orbs (due to their having a smaller span and covering a smaller area), it could be argued that stabilization is needed to protect the delicate, recently moulted spider.

[46] Walter et al. (2008) argued that "Since aciniform silk is used for both constructing web decorations and immobilizing prey, we suggest that these extensive decorations [on resting webs built just before moulting, that are not designed to capture prey] might provide a store for the swift replenishment of aciniform silk after the molt" and later use in attracting prey (p. 538). Explaining away this failure to confirm a direct prediction of the prey attraction hypothesis in this fashion is not logical. Both the metabolic costs and delays involved in reingesting stabilimentum silk, breaking it down, and then resynthesizing it (the efficiency of recycling silk, at least drag line silk, is on the order of only 30% - Tillinghast and Townley 1987) could be avoided by simply refraining from adding a stabilimentum to the resting web. In addition, if prey are indeed attracted by the stabilimentum, the spider could not derive nutritional benefit because feeding is inhibited in this context, and she would pay the additional cost of possible physical damage while she was relatively defenseless, just before and after moulting (Robinson and Robinson 1973*b*).

[47] Both inter- and intra-individual variation make a warning function less likely; the benefits from a bird's having learned from previous disagreeable encounters with other webs will be reduced if the stabilimentum designs are different.

[48] The common occurrence of inter-individual variation between members of the same species can be explained as visual defense against the possibility that a predator will learn to associate the spider with her stabilimentum (focusing, as is appropriate, on the benefits to individuals, and not to populations or species); thus building a stabilimentum differing from those of other conspecifics could improve an individual's chances of survival. Intra-individual variation however, which also seems to be common (see text), seems unlikely to have a function related to learning by predators (unless the same individual predator tends to revisit the same spider after having failed in a previous attack on a previous day; I know of no quantitative data on whether such revisits occur). This consideration weakens support for the visual defense hypothesis. Edmunds (1986) notes reasons to expect that variation is more easily compatible with the camouflage than the warning hypothesis.

[49] All four hypotheses can be modified, so that building a stabilimentum is optional depending on the amount of silk available. Obviously, a stabilimentum cannot be built when the spider lack the necessary silk.

[50] The stability, warning, and visual defense hypotheses can all, when modified to take silk reserves into account, explain this trend in terms of foraging theory: well-fed individuals are expected to divert resources into other functions rather than foraging. The prey attraction hypothesis, because it specifically deals with the spider's ability to accumulate such reserves, is less able to explain it (Blackledge 1998a,b). The authors of the *A. keyserlingi* study argued that the reduction in stabilimentum production in less well-fed spiders did not contradict the prey attraction hypothesis, but their logic is apparently based on an unconvincing use of the word "limited" ("The response of spiders in the low-prey diet appears to contradict the prediction that spiders experiencing low food levels should reduce their foraging efforts to conserve energy (Higgins 1995). However, individuals in the low-prey diet still gained weight … This means that these spiders were not food limited, but rather were relatively food deprived …"). Spider survival may not have been food limited, but their reproduction (number of eggs they could lay) very probably was. In addition, foraging theory, as noted by the authors, predicted decreased investment in foraging by well-fed animals, and these predictions were born out by the smaller webs containing less sticky silk that the well-fed *A. keyserlingi* built, on which

they made larger investments in stabilimenta. The greater investment in stabilimenta by well-fed animals is thus anomalous if stabilimentum function is to attract prey.

[51] The argument that these data do not represent a failure to confirm a prediction of the prey attraction hypothesis, because lack of stabilimenta is favorable for hungry spiders because it will reduce web damage (Herberstein et al. 2000a,b), ignores the fact that web damage due to prey is what a hungry spider *needs*; capture of food is inevitably associated with web damage.

[52] Circular stabilimenta, built more frequently by food-deprived spiders, were thought to tense radii, and thus inprove the spider's ability to capture smaller prey. Reasons to doubt this interpretation are given in Tables 3.7 and O3.4). Assuming that circular stabilimenta are more costly, the other hypotheses, when modified to take into account silk reserves give a (weak) explanation of the correlation on the basis of relative need.

[53] The substantial weight of the detritus and egg sacs would act to mechanically destabilize the web, so under the stabilization hypothesis stabilimenta should be present when egg sacs are present, not when they are absent.

[54] A possible defense of the prey attraction hypothesis, that there is a greater need for prey when sacs are absent, and a reduced need for prey when sacs are added, is not logical.

[55] I see no clear predictions by any hypothesis other than stability. More pronounced stabilimenta might be useful in darker situations for attraction, warning, or visual defense if the intended viewers have more trouble seeing them there; or they might be advantageous in lighter situations if the intended viewers would be more likely to see rather than miss them. For mechanical stability, exposure would seem irrelevant to the need for stability (unless wind damage were more likely in more exposed sites).

[56] The lack of appropriate designs for this function in the stabilimenta of many species argues that this is an incidental effect, not the function which the stabilimentum evolved to fulfill.

[57] The authors' argument that this trend favors the mechanical stabilization hypothesis are not convincing. The mechanical easons why greater stability is expected to result from having the stabilimentum below rather than above the hub were not specified: the lines that support the spider's weight are those above the hub, not those below it. In addition, the explanation for why the stabilimentum is often lacking in species like *A. argentata* was circular ("… provides the spider with a means of making a final adjustment to the mechanical state of the web *when this is necessary*") (italics added; Abstract, Robinson and Robinson 1970*a*). The contradiction with the warning hypothesis seems strong because larger, potentially web-damaging animals such as birds, would be more likely to see the upper rather than the lower portions of these webs, which are often somewhat immersed in low vegetation (the same would be true for some predators, but not others).

Table O3.5. A summary of several types of possible weaknesses in lab and field studies of the effects of stabilimenta on the attraction of prey to orbs. Some studies included more than one type of data, and are cited more than once. "Yes" means that I judged that the study suffered from the particular type of weakness, "No" that it did not. Weaknesses are classified as follows: "Lab mvts." = prey animals were observed in a highly unnatural environment from which they not have been moving in ways typical of their behavior in the field in the vicinity of orb webs (e.g., attempting to escape); "Site differences" = there was no adequate control for the possibility that differences in the numbers of prey in webs with and without stabilimenta were due to differences in the numbers of prey at different sites where spiders built (stabilimentum construction may be greater at superior sites, where previous feeding was better - see Blackledge and Wenzel 1999); "Count damages" = estimates of numbers of prey impacts were inadequate (estimated using the flawed technique of counting numbers of sites where webs were damaged (Blackledge et al. 2011; see also footnote … in Table O3.5, and discussion in sections 3.2.5.3, O3.2.3), or in some other inadequate way; "Flight patterns" = prey (bees) were tested in contexts (arriving at or leaving their nests) in which their flight patterns and speeds were probably typical of those farther afield when they encountered orbs; "Prey weight" = prey captures were quantified only by numbers of individuals, without correcting for differences in their weights or some other factor associated with their nutritive values to the spiders. "Web area" = prey capture in different webs was not corrected for the possibility that the webs had different areas covered with sticky silk[1].

Spider	Possible weaknesses Lab mvts.	Site diff.	Count damages[2]	Flight patterns	Web area[3]	Prey weight	Reference
Apparent attraction to stabilimenta							
Uloborus glomosus	YES	no	no	no	no	no[4]	Craig and Bernard 1990
Octonoba sybotides (lab)	YES	no	no	no	no	no[4]	Watanabe 1999b
(field)	no	?[5]	?[6]	no	no	YES	Watanabe 1999b
Cyclosa conica	no	YES[7]	no	no	no	YES	Tso 1998*b*
Plebs (= "*Araneus*")							
eburnus no manip.	no	YES	no[8]	no	no	YES?[8]	Bruce et al. 2004
manip.[9]	no	no[10]	no[8]	no	no	YES?[8]	Bruce et al. 2004
Argiope							
versicolor	no	YES	no	no	no	no	Li 2005
appensa	no	YES/no[11]	YES[11,12]	no	no	YES	Hauber 1998
trifasciata	no	no?[7]	YES[12]	no	no	YES	Tso 1996
aurantia	no	?[7]	no	YES[13]	no	YES	Tso 1998*a*
keyserlingi	no	no	YES[14]	YES[14]	no	YES	Blamires et al. 2001
keyserlingi[15]	no	YES/no[15]	no	no	no	YES/no[15]	Herberstein 2000
keyserlingi (lab)	YES[16]	no	no	no	no	no[4]	Bruce et al. 2001
aemula	no	no[10]	no	no	no	YES	Cheng and Tso 2007
argentata	no	YES	YES[17]	no	YES	YES	Craig 1991
argentata	no	YES/no[18]	YES	no	no/YES	YES	Craig and Bernard 1990
savignyi	no	no	no	YES	no?[19]	no[4]	Gálvez 2009
Sometimes attract, sometimes not attract							
Thelacantha brevispina	no	no[20]	no	no	YES	YES	Tseng et al. 2011
Apparent lack of attraction to stabilimenta							
Argiope							
keyserlingi[21]	no	no	no	YES	no[22]	no[4]	Rao 2010
keyserlingi (field)[23]	no	no[10]	no[8]	no	no	YES?[8]	Bruce et al. 2001

argentata[24]		no	YES	YES	no	YES?[25]	YES	Craig et al. 2001
aurantia[26]		no	no	no	no	YES	YES	Blackledge and Wenzel 1999
Gasteracantha cancriformis	field	no	no[10]	YES	no	no	YES	Gawryszewsky and Motta 2008
	lab	YES	no	no	no	no	no[4]	Gawryszewsky and Motta 2008

[1] Further variables included by Cheng and Tso (2007) that could also be important (though perhaps not so much for interception as for other aspects of prey capture such as stopping and retention) were the spacing between sticky spiral lines (the "mesh") and the numbers of radii. I have not included them in this table because the function being tested is interception (attraction to the vicinity of the orb), not capture.

[2] It can be argued that as long as the criteria for recognizing and counting damaged portions of the web were the same for decorated and undecorated orbs, the technique is reliable. There is, for instance, no logical reason that detritus damage should be higher in orbs with stabilimenta. Unfortunately, the inevitable subjectivity involved in counts with this technique (to appreciate this problem, see sections 3.2.5, O3.2.3), combined with the fact that the judgements were not made "blind" with respect to the decorated or undecorated state of the orb (and thus the possibility of unconscious bias), call into question the uniformity of the criteria in these judgements.

[3] When the areas of webs were reported (or were standardized by the techniques employed) and did not differ, or when areas differed in being smaller in the web types that captured more prey, the study was counted as having corrected for area differences. The importance of this variable is uncertain, but the finding in several studies that web area is related to the presence of a stabilimentum suggests caution.

[4] Prey were all the same species. Thus weights were similar, but the question of whether these prey were representative of all the other groups captured by the spiders remains open.

[5] Comparisons were between webs less than 1 m apart; it is not known whether prey densities differ between sites at these distances from each other.

[6] Prey capture was only determined between 14:30 and 16:00; it is not clear whether this time period is representative of the rest of the day for this species, which is active during the day (but not at night) (Watanabe 1999b). The details of how impacts were counted (perhaps by observing spiders attacking prey and feeding on them?) are not given; multiple webs were kept under observation at once so, observation must have been at least somewhat intermittent.

[7] The web "locations" (site of each spider) had similar prey numbers for decorated webs, and also similar numbers for undecorated webs. In the *Argiope* study no effects of "location" were found on prey numbers in an ANOVA analysis. But numbers of replicates at particular sites were small (total 184 webs at 53 locations), and the differential feeding hypothesis of Blackledge and Wenzel supposes that stabilimentum construction and feeding history are not independent, so the test was weak.

[8] Prey were counted every half hour, which should partially bias numbers appropriately in favor of larger prey (which take longer to consume); but most of the prey (65%) in the *A. keyserlingi* study were small (< 2mm) (sizes were not specified in the *Pleb eburnus* study).

[9] Decorated webs captured more prey at one site; but at the other site the trend (not statistically significant) was in the opposite direction.

[10] Experimental removal or painting of stabilimenta from randomly chosen orbs should correct for possible differences in web sites (even though the characterization of sites in one study with respect to vegetation density was arbitrary and not linked to prey abundance).

[11] Comparisons between entire webs did not correct for possible site differences, but those between decorated and undecorated sides of the same orb did (but the differences were nearly statistically significant: $p = 0.053$). Use of an alternative, more reliable method to count prey (number of prey being fed on by the spider and that were trapped in the webs) gave a trend (barely significant) in the opposite direction: 3 of 34 spiders with prey had decorated webs, while 61 of 253 in total had stabilimenta ($Chi^2 = 4.04$, $df = 1$, $p = 0.044$). Little confidence can be placed in these calculations, however, because different populations of spiders had significantly different frequencies of stabilimenta, and the populations in which spiders were seen with prey were not specified. In addition, there was no significant difference in the number of trapped prey items between decorated and undecorated sides of the same orb ($p = 0.33$, $N = 50$). This also reduces confidence in the author's conclusion that the prey attraction hypothesis was supported.

[12] Wrapped prey were also included in the counts.

[13] Both the artificial frames on which the stabilimenta were mounted and the artificial traps on which they were placed differ greatly in visibility from orbs, at least for humans.

[14] Webs without spiders were used, so only prey that had failed to escape between the hourly observations were counted. There was thus probably a strong bias toward small, weak prey compared with captures by spiders on their webs.

[15] Smaller prey that the spider had partially consumed could not be measured, and some prey that took <30 min to consume would have gone unrecorded (inspections were made every 30 min). Prey capture correlated with web decoration on only two of three days. In some analyses there was no control for the possible effects of web site; in others site effects were tested using changes in prey captures (but using only numbers of prey without correcting for size) for spiders that increased or decreased the number of arms in the stabilimentum from one day to the next, and were marginally significant ($p = 0.04$ with a two-tailed test, as was appropriate in view of the mix of confirmation and lack of confirmation of the prey attraction hypothesis). The orbs were also smaller when the stabilimentum decreased than when it increased (though not significantly so: 622 ± 59 vs 710 ± 65 cm^2; $p = 0.08$). The numbers of prey/cm^2 were not compared for these webs, and the combination of the barely significant and barely not significant differences leaves in question whether differences in prey/cm^2 were significant. In sum, some conclusions from this study are open to doubts.

[16] The likelihood that prey may have been attempting to escape was mentioned by the authors.

[17] The uncertainty associated with this technique may have been less serious in this study compared with that in others, because experiments were ended "… when webs became so damaged that it was impossible to determine accurately the locations of all new interceptions." (p. 650,

Craig 1990); but this level of damage was not specified concretely, and is very difficult to determine (see footnote [2] and the caption for this table).

[18] Use of decorated and undecorated halves of the same web comes close to standardizing for possible site effects; but these effects were not taken into account in the whole web comparisons.

[19] The frames used were standard size; but they were large enough (34.5 x 45 cm) that it is not certain that all the enclosed area was covered by the orb.

[20] The effects of the technique used to reduce stabilimentum visibility (blackening them) have not been demonstrated for either predators or prey.

[21] A similar lack of effect was obtained using the honey bee *Apis mellifera* instead of stingless bees (D. Rao, pers. comm.).

[22] The hoops into which orbs were affixed were of a standard size, and all orbs filled them completely (D. Rao, pers. comm.).

[23] Decorated webs did not capture significantly more prey than those lacking stabilimenta (see also Table O3.3 and Rao 2010 for different types of evidence not in accord with the prey attraction hypothesis). The authors nevertheless concluded that stabilimenta attracted prey, on the basis of calculations based on estimates of the abundance of “available” prey that were obtained using artificial traps placed near the orbs. There are various serious problems, however, with using such traps to measure available prey (discussed in detail in Eberhard 1990*b*; see also sections 3.2.5.4, O3.2.3). Thus it is not clear whether these corrections were necessary, nor whether they justify this modified conclusion.

[24] In the authors’ words, “There was no suggestion of a decoration effect (decoration presence or absence), N = 2, F = 2.3, df = 1, P = 0.11)”. They argued, nevertheless, that “… the extreme spatial and temporal variability that characterizes the web sites of *A. argentata* … will mask the effect of the presence or absence of web decorations [on] the rate of prey interception”. The crucial question, however, is not whether the variability was large enough to mask the effect, but whether or not it actually did mask an effect. In the absence of a reason to suppose that such masking occurred (none was given), it seems more parsimonious to me to take the data at face value.

[25] The Methods section of this paper indicated that web sizes were measured, but there is no mention of their possible effects in the Results.

[26] There was a significant trend in the direction opposite that predicted by the prey attraction hypothesis: 34% fewer prey were captured on webs with stabilimenta. This is thus strong evidence against the prey attraction hypothesis.

Table O4.1. The mix of correlations and lack of correlations between the design features of the webs and attack speeds in a small, somewhat arbitrary sample of species with particularly rapid and particularly slow attacks. The species that were chosen have either extreme web designs or extreme attack behavior. The "compensatory co-evolution of web and attack behavior" hypothesis predicts that species with web designs that are especially well-designed to retain prey will have especially slow attack behavior, and vice versa. Attacks on very large, dangerous prey are not included (all species approach these slowly) ("stsp" = sticky spiral). Five of the eight contradictions may be eliminated when the physical properties of the lines are taken into account (marked with "*") (see footnotes).

Species	Retention potential of web design	Attack speed	References for web properties	References for attack behavior
Support coevolution hypothesis				
NON-ORB WEBS				
Hypochilus gertschi (Hypochilidae)	High (strong lines, strong adhesion)	Slow[1]	Shear 1969	Shear 1969
Theridium evexum THD	High (strong lines, strong adhesion)[2]	Slow[1]	Barrantes and Weng 2007, WE	Barrantes and Weng 2007, Barrantes and Eberhard 2007
ORB WEBS				
Scoloderus tuberculifer AR	High (many, dense stsp lines	Slow[1]	Eberhard 1975	Eberhard 1975
Gasteracantha cancriformis AR	Medium-high (strong lines, sticky)	Slow[1,3,4]	Hénaut et al. 2001, WE	Eberhard 1989, WE
Micrathena spp. AR	Medium-high (strong lines, sticky)	Slow[1,3]	WE	WE
Leucauge mariana, L. venusta TET	Low (weak, low stickiness)	Rapid[1,5]	Hénaut et al. 2001, Zschokke et al. 2006, WE	Zschokke et al. 2006, Briceño and Eberhard 2011, Eberhard 1989
Contradict coevolution hypothesis				
NON-ORB WEBS				
**Phoroncidia* spp.	Low (single sticky line)[6]	Slow[1,3]	Shinkai and Takano 1984, Eberhard 1981*b*, WE	Eberhard 1981*b*, WE
ORB WEBS				
Cyclosa sedeculata AR	Low[7]	Slow[1,7]	Miyashita 1997	Miyashita 1997
Hypognatha sp. AR	Medium-low (medium sparse, webs in tatters soon after construction)	Slow[3]	Eberhard 1986*a*, WE	WE
**Cyrtarachne* spp. AR[8]	Low (sparse sticky lines)[6]	Slow[3]	Cartan and Miyashita 2000	Cartan and Miyashita 2000
**Mangora* spp. AR	High[9] (very dense stsp)	Rapid[1]	Sensenig et al. 2010[9]	WE
Nephila clavipes NE	High (strong lines, dense stsp	Rapid[1]	Zschokke et al. 2006, Sensenig et al. 2010	Robinson and Mirick 1971, Zschokke et al. 2006, WE
**Hyptiotes* spp. UL	Low[10] (sticky lines mod. sparse)	Slow[1,3]	Marples and Marples 1937, Opell 1982	Marples and Marples 1937, WE
**Theridiosoma* spp. TSM	Medium-low (sticky lines mod. sparse)	Slow[1,3]	Comstock 1967, Coddington 1986*a*	McCook 1889, WE
**Olgunius* spp. TSM	Low (very sparse sticky lines)	Slow[1,3]	Coddington 1986*a*, Eberhard 1986*a*	WE

[1] Direct observations of attacks

[2] Lines are sparse however, lowering retention potential

[3] The legs very short for the body size, so rapid attacks are not possible

[4] median delay to reach prey was 8 s (mean 15.9 ± 23 s, N = 24)

[5] median delay to reach prey was 1 s (mean =2.5 ± 3.0 s, N = 23)

[6] adhesiveness of sticky lines was apparently strong; if this is taken into account, contradiction of hypothesis may be eliminated

[7] compared (Miyashita 1997) with respect to orbs and attack behavior of two other co-occurring species of *Cyclosa, C. octotuberculata* and *C. argenteoalba.*

[8] The related genera *Pasilobus* and *Poecilopachys* also with sparse webs and stubby legs

[9] Adhesiveness with respect to the total web area is low; thus, because the density of sticky lines is high, the stickiness of individual lines is probably low and the classification as high retention capacity may be incorrect.

[10] The spider’s ability to collapse the web when prey strike probably substantially increases the chances of retention, so if this is taken into account, the contradiction is uncertain.

Table O6.1. This undoubtedly incomplete list of the "vocabulary" of different motor patterns used during the early stages of orb construction by a few arbitrarily chosen species illustrates the complex combination of behavioral traits utilized to build an orb web. Behavior early in orb construction is relatively poorly studied, so lack of reports of particular behavior patterns may have little significance. Interspecific comparisons may be informative when better data become available,

Behavior (possible function)	species	Reference
During Exploration:		
Destroy frames from day before	*M. duodecimspinosa*	WE
Destroy only radii, stsp and hub from day before	*A. bifurca*, *Cyclosa turbinata*, *Metabus ocellatus*	Carico 1986, WE, J. Moya in prep. Buskirk 1975
Descend without attach	*M. duodecimspinosa*	WE
Descend as break and reel	*A. diadematus, M. duodecimspinosa*	Zschokke and Vollrath 1995a,b, WE
Shift attachments (break, move sideways)	*M. duodecimspinosa*	WE
Attach "around the corner" to the substrate	*M. duodecimspinosa, N. clavipes* *U. diversus, P. vicina*	Eberhard 1972, 1990*a*
Reinforce frame lines	*U. diversus*	Eberhard 1972
Fish for new attachments by floating lines		
while hanging on vertical line	*P. vicina*, *M. duodecimspinosa*	WE
while sagging horizontal line	*M duodecimspinosa*	WE
Remove and ingest tufts of silk	*M duodecimspinosa*	WE
Reel up fishing line and make tuft	*M duodecimspinosa*	WE
During construction of hub, primary radii, frames, and anchors:		
Build distinct proto hub with hub loop?		
Yes	*U. diversus, P. vicina*	Eberhard 1972, 1990*a*
No	*A. diadematus, M. duodecimspinosa*	Zschokke 1996, Zschokke and Vollrath 1995a,b, WE,
Sometimes multiple convergences radial lines early on and all but one later removed	*M. duodecimspinosa*	WE
Protohub replacement and imm. eat fluff and sew together broken radii	*P. vicina*, *U. diversus*	Eberhard 1972, 1990*a*
Remove radii partially/completely) leading up to protohub replacement	*U. diversus*, *P. vicina*	Eberhard 1972, 1990*a*
Add frames prior to proto hub replacement		
Add frames and modify radii (primary) in strict order just before protohub replacement	*U. diversus*, *P. vicina*	Eberhard 1972, 1990*a*
Shift distal attachment of radius during frame const.	*M. duodecinspinosa*	WE
Replace inner end radial lines	many Araneidae, Tetragnathidae, Theridiosomatidae, Anapidae Mysmenidae, Symphytognathidae	Eberhard 1982, 1987*c*, 1990*a*, Zschokke and Vollrath 1995a,b Zschokke 2000b
Diversity of types of frame construction		
low	*L. mariana, P. vicina*	Eberhard 1990*a*
high	*N. clavipes*	Eberhard 1990*a*

Table O6.2. Comparisons of the sequences in which different operations in web construction were performed by different taxa of orb weaving spiders. Some operations are performed in the same sequence throughout all orb weavers (A). For some other operations, different taxonomic groups differ in the order in which they perform the same operations (B). There are, in addition, many sequences which are mechanically feasible but which have never been observed (C) (this list of unobserved sequences is undoubtedly incomplete). The apparent consistency among the three, symphytognathoid families may be an illusion, due to poor sampling. Data based mainly on the summaries of Witt et al. (1968), Eberhard (1982, 1987*c*), Vollrath (1992), and Ramírez et al. (2004); "tsp" = temporary spiral; "stsp" = sticky spiral; "-" = not applicable).

Behavioral sequence	Ulob.	Nephil.	Aran.	Tetragn.	Theridio.	Anap.	Symphytogn.	Mysmen.
A. "Typical" sequences								
Sticky lines laid starting at outer edge and working inward	yes	yes	yes	yes	yes	Yes	yes	yes
No further exploratory behavior once frame and radius construction begins	yes	yes	yes	yes	yes	Yes	yes	yes
Hub built before tsp (tsp after hub)								
All frame lines built simultaneously with a radius	yes	yes	yes[1]	yes	yes	Yes	yes	yes
Tsp laid starting at hub and working outward	yes	yes	yes	yes	yes	Yes	yes	yes
B. Sequences that differ between groups								
Destroy center of hub after finish stsp	no	no	yes	yes	no	no	no	no
Destroy and rebuild entire hub after stsp	no	no	no	no	yes	yes	yes	yes
Add radii after finish stsp	no[2]	no[3]	no	no	no	yes	yes	some
Begin hub spiral construction during radius construction	yes	yes	some	no	no	no	no	no
Lengthen radii after stsp construction	no	no	no	no	yes	yes	yes	yes
Add radii after begin tsp	some	yes	some	no	no	no	no	no
Omit tsp	no	no	no	no	some	yes	yes	yes
Transition from hub spiral to tsp is gradual	yes	yes	some	no	no	-	-	-
C. Sequences unknown in any orb weaver								
Destroy or reinforce center hub after tsp but before stsp construction	no	no	no	no	no	no	no	no
Alternate building radii w. and w.o. adding hub loops	no	no	no	no	no	no	no	no
Add to or reinforce frame lines at any stage after radius construction	no	no[2]	no	no	no	no	no	no
Interrupt stsp to build any structure with non-sticky silk and then resume stsp	no	no	no[4]	no	no	no	no	no
Tighten a radius after it has been built (other than via zig-zag hub or tsp lines)	no	no	no	no	no	no	no	no
Reduce tension on any frame line after it is built	no	no	no	no	no	no	no	no
Return to the hub along the exit radius rather than along the new radius after attaching a new radius to a frame line	no	no	no	no	no	no	no	no

---

[1] There are some exceptions in *Araneus diadematus* (Zschokke 1996)

[2] Second instar nymphs of *Uloborus* and *Philoponella* add many thinner radial (and non-radial) lines after tsp construction (they do not build sticky spiral lines) (Szlep 1961, Eberhard 1972, 1977) (see Fig. 9.20).

[3] *Herennia* builds unique, synapomorphic, "pseudoradii" that run from the upper to the lower edge of the web and to which sticky spiral lines are attached (Fig. 4.3). The behavior used to produce these lines, which would seem to be more appropriately termed frame lines than radii because they are not oriented in radial directions, has not been described, and many questions remain (Are they built before or after the normal radii? Does it include components of normal radius construction?). In the photograph of the web of a juvenile in Robinson and Lubin (1979), in contrast, the sticky spiral lines appear to be attached to the "true" radii and not the pseudoradii; this is also clear for a few attachments (at least near the side of the retreat) (Fig. 4.3, Kuntner 2005).

[4] Can be induced by damaging webs during sticky spiral construction in *Micrathena duodecimspinosa* (AR) (WE)

Table O6.3. Uniformity from diversity: the movements and probable mechanical functions of the legs of the araneid *Micrathena duodecimspinosa* (AR) during construction of the outer loops (2-6) of the sticky spiral. The behavior and functions of most legs varied depending on whether the spider was above or below the hub; movements and probable mechanical functions differed in still additional ways in other areas of the web (e.g., descending or ascending even with the hub rather than above or below it), and at different distances from the hub. For instance inner legs I-III made fewer steps/attachment when the spider was closer to the hub (where the distances between radial lines were much smaller); in constrast, her outer legs continued to make one new step/attachment even near the hub. The degree of difference in forces exerted by her legs above and below the hub, and the relative importance of the function of pushing the spider's body away from the web (to avoid entanglements) must have both been greater in more nearly vertical orbs (the slants of 70 webs in nature ranged between 59 and 90°). The probable functions for each leg were deduced from the following types of data: displacements of web lines when they were grasped by the leg (e.g., support the spider's weight if line was bent sharply downward toward spider's probable center of gravity (anterior portion of her abdomen); the position of the spider's body with respect to these directions of displacement (e.g., push web away from her body, support her weight). The force that propelled the spider around her web also varied with her position (mostly gravity as she descended; strong pulls with her anterior legs as she climbed; moderate pulls on lines when she was directly above and below the hub (as in the observations in this table) (some other, more subtle mechanical functions, such as keeping the spider's ventral surface more or less parallel to the web plane, and handling segments of the tsp as they were being broken, were not taken into account); and the details of the leg movements (for instance, repeated tapping that immediately ceased when a new line was touched and that was then followed immediately by a change in behavior such as grasping the line or turning her body to make an attachment was interpreted as indicating that the tapping had functioned to locate a line). One "step" included the movements between releasing a grip on a line at one site to grasping a line at another site. When one leg followed another leg's steps in time and space, the movements of the leading leg that led to localizing the line that it then grasped were taken to function as "guiding" the following leg. In "hand-over-hand" movements, each of the two legs probably guided the other to some extent, but each leg also had to explore to encounter the line to grasp it. No experiments were performed, so these deductions regarding functions are tentative. In sum, the extreme uniformity of the spider's sticky spiral construction behavior at one level of analysis (*always* attached to the radius, *always* moved via the temporary spiral to the next radius, *always* located the inner loop of sticky spiral, *always* grasped the radius with legs III and IV, and *always* then attached) was underlain by large variations in the motor behavior and the functions performed by different legs. ("tsp" = temporary spiral; "stsp" = sticky spiral; "r_{n-1}" = the last radius to which the sticky spiral was attached; "r_n" = the next radius to which which the sticky spiral will be attached; "r_{n+1}" = the radius beyond r_n; in "hand over hand" movements, legs alternate in grasping the same line, with each leg apparently finding the line on its own and neither leg obviously leading the other; **bold** indicates functions that differed above and below the hub. Note that the label of a radius changed the moment a new attachment was made; for instance, r_{n+1} became r_n.

Leg	Spider was within 30° of directly ABOVE THE HUB	Spider was within 30° of directly BELOW THE HUB
iI	Movements: step along tsp between r_{n+1} and r_{n+2} (sometimes hand-over-hand with iII or less often with oI); 1-2 steps/attachment Functions: **push to maintain distance from orb (small force, extend)**; guide iII to tsp(?); **propulsion (small force, flex)**	Movements: tap and step along tsp just short of r_{n+1} hand-over-hand with iII (early loops) or on r_{n+1}) last loops (sometimes not follow other leg); one step/attachment Functions: **sustain some of spider's weight (mod. force, contract)**; occasionally guide oI, often guide iII (approximately) to tsp
iII	Movements: reach for and grasp tsp or (more often) r_n inside tsp; 1-2 steps/attachment Functions: **push web to maintain distance from tsp and r_n (small force, extend)**; guide iIII to tsp; **propulsion (small force, flex)**	Movements: follow (approximately) iI but grasp tsp or r_n just beyond the site on the tsp held by iI or just outside of the site on r_n (rather than tsp); alternatively, move hand-over-hand with iI along tsp; one step/attachment Functions: **sustain much of spider's weight (strong force, contract)**; guide (approximately iI or iIII to tsp or (sometimes) r_n
iIII	Movements: grasp r_n or tsp near junction with r_n (follow iII), pull on tsp (moderately weak force, contract); number of steps/attachment unsure[1] Functions: **maintain spider's distance from web by pushing on r_n or tsp (bend them upward) (moderately weak force, contract)**	Movements: follow iII (grasp r_n or tsp just behind it); one step/attachment Functions: **sustain spider's weight (moderate force, flex)**
iIV	Movements: push new stsp segment away from spinnerets just before and during attaching it (Fig. 6.24); then imm. grasp r_{n-1} and perhaps push against it, then reach forward to grasp new segment of stsp.; two steps/attachment Functions: lengthen stsp segment; **maintain spider's distance from orb or propulsion**	Movements: grasp and push new stsp segment once ventrally and away from the spinnerets just begore attachment was made; NOT grasp rn-1 (instead stay in the air following attachment) and release of stsp, then move to grasp next stsp segment; one step/attachment Function: lengthen segment stsp

oI	Movements: tap ahead to tsp or r_{n+1} (not follow any other leg); sometimes touch inner loop stsp (but not responses by spider); 1-2 steps/attachment Functions: guide oII; locate inner loop (sometimes); **sustain spider's weight on tsp or rn; pull anterior end spider upward (mod. force, contract)**	Movements: tap outward toward inner loop (sometimes hit it, but usually not), then grasp r_{n+1}, tsp, r_n, or sometimes just wave in the air; one step/attachment Functions: sometimes pull spider forward (bend r_{n+1} toward the spider); locate inner loop stsp (sometimes); guide oII to r_n or vicinity; **propel spider forward (small force, flex)**
oII	Movements: sometimes follow oI to r_{n+1} (grasp it outside of oI), or sometimes find r_n and grasp it on its own; one step/attachment Functions: **sustain most of spider's weight at some moments (strong force, flex)** (Fig. 6.24), guide iIII to r_n	Movements: follow oI to grasp r_n or tsp, or move hand-over-hand with oI, or find rn on its own with a more exploratory wave; one step/attachment Functions: guide oIII to r_n; **not sustain spider's weight but probably pull on r_{n+1} to move forward (weak force, flex)**
oIII	Movements: follow oII to r_n (grasp outside of oIII); one step/attachment Functions: **sustain weight of spider (strong force, flex);** pull on r_n to raise abdomen, and to align spinnerets with r_n in order to make an attachment (mod. force, contract); guide oIV to r_n	Movements: follow oII to r_n (grasp r_n inside of oII), one step/attachment Functions: align spinneerets with r_n and pull abdomen up toward it to contact the spinnerets for attaching (medium force, flexion); guide oIV to r_n
oIV	Movements: follow oIII to r_n and then slide outward to touch inner loop (sometimes stops short); one step/attachment Functions: locate inner loop of stsp **(less often)**; pull on r_n to raise abdomen, and to align spinnerets with r_n in order to make an attachment (mod. force, flex); **sustain spider's weight just after attachment (strong force, contraction)**	Movements: follow oIII to r_n and slide along it outward to grasp it behond oIII, pull abomen up toward spinnerets for attachment; one step/attachment Functions: locte inner loop of sticky spiral **(more often)**; hold and align r_n with spinnerets to permit attachment; pull abdomen up toward r_n (moderate force, flex)

[1] It was not always possible to distinguish brief grasps of the temporary spiral from simple contacts

Table O8.1. Mean height of the hub above the ground (± one standard deviation) for a sample of 14 species in four families (mostly from Valderrama 2000, in a high elevation tropical forest). In general field data on web height are likely to be biased due to more thorough searches near head height (between about 1.5 and 2.5 m). But these data are likely to have less strong bias than in many other studies, because Valderrama climbed trees to search for webs; and the webs of *Uloborus diversus* were found by kneeling next to low (1-1.5 m tall) piles of debris (pack rat nests) on the Sonoran desert. Unless otherwise specified, all data are for adult females. The nymph sizes for *U. diversus* do not necessarily correspond to instars; the data for this species were estimated from graphs, and do not permit calculation of standard deviations (c = clearing, y = young forest, o = old forest).

Spider	Habitat	Mean height (cm)	N	Reference
Araneidae				
Araneus bogotensis	o	149 ± 92	19	Valderrama 2000
Azilia sp.	c	40 ± 21	22	Valderrama 2000
Azilia sp.	o	169 ± 142	26	Valderrama 2000
Azilia sp.	y	23 ± 8.6	46	Valderrama 2000
Cyclosa caroli	c	128 ± 75	13	Valderrama 2000
Cyclosa caroli	o	130 ± 78	27	Valderrama 2000
Micrathena pilaton	c	74 ± 20	14	Valderrama 2000
Micrathena pilaton	y	114 ± 37	18	Valderrama 2000
Micrathena pilaton	o	105 ± 73	27	Valderrama 2000
Parawixia rimosa	o	122 ± 73	30	Valderrama 2000
Tetragnathidae				
Chrysometa otavalo	y	85 ± 33	14	Valderrama 2000
Chrysometa otavalo	o	118 ± 73	33	Valderrama 2000
Chrysometa sp.	c	57 ± 25	15	Valderrama 2000
Chrysometa sp.	y	66 ± 55	40	Valderrama 2000
Glenognatha sp.	y	122 ± 35	15	Valderrama 2000
Glenognatha sp.	o	152 ± 16	10	Valderrama 2000
Theridiosomatidae				
Epeirotypus sp.	o	146 ± 64	64	Valderrama 2000
Naatlo sutila	c	79 ± 42	60	Valderrama 2000
Naatlo sutila	y	99 ± 74	82	Valderrama 2000
Theridiosoma sp.	y	190 ± 130	13	Valderrama 2000
Theridiosoma sp.	o	161 ± 86	23	Valderrama 2000
Uloboridae				
Uloborus diversus nymph 1	o	24	29	Eberhard 1971*a*
Uloborus diversus nymph 2	o	27	52	Eberhard 1971*a*
Uloborus diversus nymph 3	o	30	110	Eberhard 1971*a*
Uloborus diversus adult	o	27	97	Eberhard 1971*a*

Table O10.1 Important but easily-filled gaps in current understanding

This table is meant to be a shotgun, online shopping site for students and teachers who are searching for simple, publishable projects to perform with web weaving spiders. It is a roadmap to apparently easily-initiated projects (whose preliminary results will undoubtedly lead to additional questions) and fill in gaps in our knowledge. The topics range from major questions to simply filling in details, but there are at least the beginnings of many possible Masters and PhD theses. The list is obviously biased toward questions that I find interesting, toward species mentioned frequently in this book (the reader can supply other species in the same groups that happen to be available), toward simple techniques that require little in the way of specialized equipment, and (to some extent) toward the heretofore neglected non-orb weavers. It is organized in rough accord with the chapters of the book. If I could look forward to living long enough, this table would constitute a "To Do" list for me; lacking solutions on this score, I hope that it may help others to find interesting unanswered questions.

A. The designs of orbs and their functional significance

A1. Mechanical and chemical properties of silk lines and orb designs

- What is the correlation (and the lack of correlation) between web design features and differences in the biomechanical properties of different silk lines among individuals of the same species, and in different species with different web designs?
- Are there ontogenetic differences in the chemical compositions and mechanical properties of the different types of lines in orbs?
- Is the chemical composition of the sticky silk used by theridiids to wrap their prey (presumably from the aggregate and flagelliform glands) similar to the sticky silk in araneoid orbs?
- Do spiders in the *Cyrtarachne* group of genera produce chemical prey attractants (how can their apparent strong specialization on moths, but lack of specialization on particular species or species groups of moths be explained)?
- Does the scaling of thread diameters, sticky droplet diameters and inter-droplet distances, or cribellum puff diameters and inter-puff intervals change with spider size? Do they vary between taxonomic groups?
- Is the non-linear mechanical response of ampullate silk lines to stress an adaptation that was acquired after orbs evolved, or was it a pre-existing trait in non-orb spiders that orb weavers evolved to exploit (e.g. Cranford et al. 2012) (compare silks of different taxa)?
- How much of the stickiness of araneid sticky spiral glue washed off with different intensities of rain/fog? How large must the droplets of fog condensed on lines be to affect the distribution of glue droplets on the lines?
- Is the distance between puffs on the sticky spiral greater in the outer loops (as Crews and Opell 2006 found with the sticky droplets of *Cyclosa turbinata*)?
- Are there correlations involving humidity optima for sticky silk in different species and their building times that support the hypothesis that building times are adjusted to occur at humidities that give greater stickiness?
- Are the numbers and diameters of strands in radii, frames, etc. consistent intra-specifically? Do they vary with spider size? between different species?
- Are the chemical and mechanical traits of lines consistent in different parts of same orb, and in the same parts of the orbs in a wide array of different species (extend Sensenig et al. 2011a)?
- Are there adaptive variations in supercontraction between species that live in habitats with different humidity regimes, or between conspecific individuals in habitats that differ in humidity?
- Are there differences in the silk properties of *N. clavipes* in populations in Mexico and Panama that correlate with the other ecological and behavioral differences demonstrated by Higgins?

A2. Functional consequences of different orb designs

- Do greater numbers of radii correlate with a reduction in the larger-near-the-edge pattern in the sticky spiral spacing (as predicted by the radius density hypothesis) when the orbs of many different species are compared?
- Do first and second *L. mariana* webs of the day have an accentuated edge-to-hub patterns of sticky spiral spaces (as predicted by the radius density hypothesis, because they have fewer radii) (the "running out of silk" hypothesis predicts a reduction in the pattern)? Does this pattern change when the second web is made with full sticky spiral glands (perhaps, if the spider tends to be running out of sticky silk when finishing the sticky spiral in normal second webs, with tighter spacing near the hub)?
- Can any of the multiple explanations for how cribellate fibrils adhere to insects explain why certain spiders (including the scytodid *Scytodes* and the salticid *Portia*) failed to ahere to cribellate silk, and why the calamistrum and the posterior lateral spinnerets also fail to adhere to them during production of these fibrils?
- Are there any web design traits that correlate intra- or inter-specifically with zig zag attachments at the hub? Do the sizes of the zig-zags correlate intra-specifically with web design traits? with spider hunger in uloborids (see Wantanabe 2000)? with the order of radius construction (as supposed in *Uloborus diversus* – Eberhard 1972)?
- Do smaller individuals show any signs of having special problems regarding energy expenditure compared with larger stages of same species (as predicted by their relatively larger and thus energetically more expensive brains)?
- Is it possible to raise young *Uloborus* or sustain mature males on pollen (thus explaining their unusual, highly dense orb designs)?
- Are the retention times in perfectly vertical orbs longer than those in orbs that are slightly slanted (75-80°)?
- Is the amount that the hub and radial lines sag when the center of the hub is removed greater in vertical orbs (especially in the vertical direction) than in other webs (e.g., do spiders build vertical orbs under more tension to avoid sagging problems during sticky spiral construction)?
- Is the fact that partial web replacement is more common in adult *Nephila clavipes* than in earlier instars (Higgins and Buskirk 1992) associated with relatively greater material investments in orbs in adults (web size, density of lines, diameters of glue droplets and lines)?

- How do the prey of *Metabus* flying in the late afternoon (when building behavior peaks) differ from those at other times of the day, and are they likely to produce less stressful impacts than those at other hours (as predicted by the less dense webs built at this time of day)?
- What are the precise relationships between wind velocity, lengths of radii and sticky spiral lines, and the amount of sag in lines and in the entire web, and how do these values in nature relate to the spaces between sticky spiral lines?
- Does wind striking an orb perpendicularly pose less of a threat with respect to damage from lines adhering to each other (especially spiral adhering to radius) than wind at more acute angles?
- Do retention times increase when the tensions on an orb are reduced (by bending a flexible frame)? Do they decrease if the web is tensed?
- How do ecological factors (such as prey availability) that are associated with the changes in spider size from spiderling to adult correlate (or fail to correlate) with ontogenic changes in web design (are ontogenetic changes in web designs often constrained ecologically rather than by phylogenetic inertia)?
- Is the relaxation of web tensions particularly dramatic in species with fewer radii and sticky spiral loops when the center of the hub is removed at the end of construction (during sticky spiral construction the spider's weight would be supported by fewer lines and would thus cause more distortion, so these species might need to have especially tense webs during construction?
- Is the relaxation of web tensions when the center of the hub is removed particularly dramatic in perfectly vertical orbs (species that build more nearly vertical orbs build particularly tense lines early in construction, since the problems from sagging under the spider's own weight are greater because her body will sag into web lines directly below her as she works)?
- Do hub lines sag a greater amount when the center of the hub is removed greater in short-legged vs long-legged species (e.g., do short-legged species make webs tighter during sticky spiral construction to avoid problems of sagging under their own weight, because they cannot disperse their weight by grasping lines that are farther apart)?
- Will collections of the prey of ray-web theridiosomatids that spring their webs show that they tend to capture nematocerans and other prey with tentative flight patterns, as has been supposed? Will elimination of spring lines in the field change this trend, and reduce their overall prey capture success?

A3. Testing explanations of the functional significance of the "larger-near-the-edge" pattern in sticky spiral spacing

- Is there an accentuation of the "larger-near-the edge" pattern in groups with radius-poor webs, such as those of *Tetragnatha lauta*, *Metabus*, and theridiosomatids in general (predicted by the radius density hypothesis)? Is there a reduction of this pattern in species with radius-rich webs, such as *Cyclosa* spp., *Micrathena sexspinosa*, *Zosis geniculata* (also predicted by this hypothesis)?
- Does the "larger near the edge" pattern decrease when a large object is placed experimentally near the orb (presumably reducing prey velocities)? Do similar within-species correlations occur in the field in species (such as *Allocylosa bifurca*) in which some but not all webs are built very near large objects (also, are there ontogenetic changes in the effects of sites with such objects)?
- Do webs of other species that have tangles beside the orb (such as *Araneus pegnia*, *Araneus cingulatus*, *Araniella cucurbitina*, *A. displicata*) have reduced edge-to-hub differences in sticky spiral spacing similar to that seen in *Metepeira* sp.?
- Does the spacing at the sides of vertical webs, where tumbling will not favor tighter spacing, show a reduced larger-near-the-edge pattern compared with above and below the hub (predicted by the tumbling hypothesis to explain the larger-near-the-edge pattern in sticky spiral spacing)?
- Do second instar *Nephila* have the same lack of a "larger-near-the-edge" pattern of sticky spiral spacing as adults?
- Do symphytognathoid species like *Patu* with huge numbers of radii show a reduced "larger-near-the-edge" trend in sticky spiral spacing. as compared with species with low numbers of radii like *Anapisona* (an independent test of the radius density hypothesis in symphytognathoids)?
- Do the uloborids and the anapids which typically build in constrained spaces and which typically lay sticky spiral lines near or on frame lines, have any compensating traits that would make up for the loss of extensibility of these sticky lines and their greater danger of adhering to frame lines?
- Do second *L. mariana* webs of the day have accentuated "larger-near-the-edge" pattern of sticky spiral spaces (as predicted by the radius density hypothesis, because they have fewer radii) (the "running out of silk" hypothesis predicts the opposite - a reduction in the pattern)? Does this pattern change when the second web is made with full sticky spiral glands?

A4. Possible taxonomic patterns

- Do estimates of the relative size of the space spanned compared with the size of the web (for instance, longest frame/mean diameter of capture zone) vary between congeneric species, or genera (a preliminary impression is that there are "large space" groups such as *Gasteracantha, Caerostris, Hypognatha* and some *Micrathena* [AR], "moderate space" groups like *Argiope* [AR] and *Uloborus* [UL] and tiny space groups like *Anapisona*)?
- Are the patterns of temporary spiral spacing with repect to the distance from the hub, and above and below the hub similar in different taxonomic groups? Do they change ontogenetically?
- Do the relative numbers of secondary frames vary in different taxonomic groups; in particular, do uloborids tend to build fewer secondary frames (as seems to be the case)?
- Do the relative numbers of tertiary radii (as compared with total radii) vary in different taxonomic groups?
- Do uloborids usually leave more temporary spiral segments unbroken than araneids? Are intact temporary spirals completely lacking in tetragnathids?
- Do unbroken segements of temporary spiral tend to be farther from the hub in uloborids than other groups?
- Do the immediate responses to prey (e.g. run to prey vs. turn and jerk) vary according to the taxonomic groups of orb weavers?
- Do different taxonomic groups differ with respect to whether the spider holds radii in the free zone rather than lines in the hub as she waits for prey at the hub?

- Do different taxonomic groups differ with respect to holding the web tense (bending lines) while waiting for prey (*Nephila* and uloborids seem to hold hub lines and not to tense the web)?
- Will quantitative measures confirm the impression that uloborids differ from araneoids in laying more sticky lines on and beyond frame lines?
- How large are the intra-specific compared with the inter-specific variations between congeneric species in different aspects of orb web designs under natural and laboratory conditions (variations in nature and under uniform conditions are both of interest, in the contexts of, respectively, ecological and behavioral evolution)? How large are the intra-generic vs the inter-generic differences?
- Do other orb-weaving groups such as nephilids and theridiosomatids use the same stimuli to guide web construction and respond in the same ways to them as *Leucauge* and *Zosis* (e.g., repeat Hingston expts (already done by Peters with *Nephila*), changes in the amounts of silk available, break radii, change TSP-IL distance, etc.)?
- Is there a relation between the lengths of legs and the density of sticky spiral lines (both scaled on spider size), and does it correlate with the phylogeny of orb weavers?
- Are there phylogenetic patterns of the ontogentic changes in orb design vary in different groups? Do these changes correlate with other factors in ways that might explain why they differ in different species?
- Does the correlation (intra-specific; inter-specific) between the number of hub loops and the number of radii vary in different taxa? Are there phylogenetic patterns in the correlations?
- Are there phylogenetic patterns in the relative size of the free zone? Are there correlations between the relative free zone size with other aspects of orb design?
- Are there phylogenetic patterns in the degree to which spacing between sticky loops increases at the inner edge of the capture zone?

A5. Patterns in the evolution of orbs

- Do the magnitudes of intra-specific variation in different web traits correlate with inter-specific differences among congeners (is divergence correlated with intra-specific variability)?
- Is there variation among species in how much the space available needs to be constrained for the spider to begin to attach sticky lines to frame lines and to lay them outside the frames? Does this variation correlate with the sizes of typical websites utilized in nature?
- Are the orbs of species that turn quickly at the hub but only later move more slowly to the prey (e.g., *Micrathena, Gasteracantha*) more symmetrical (as predicted if speed in reaching the prey is less important) than those of species that turn and run to the prey quickly (*Leucauge, Nephila, Neoscona*)?
- Is there any relation between the evolutionary divergence in leg movements in orb weavers and the ability to adjust behavior to compensate for leg loss?

A6. How orbs break (using marbles or similar objects with different weights and velocities)

- Do the radii in a typical web always break at the site of impact, rather than at their attachments to the frame or the the hub, or only at impact site on radius)? Does this vary in webs with intact temporary spiral lines (such as *Nephila* or *Cyrtophora*) (as might be predicted by Aoyanagi and Okumura 2010 or Cranford et al. 2012)?
- Do the sites of breakage and the sizes of the holes change (become more localized) if the temporary spirals are removed from *Nephila* webs?
- How do the lines that are broken when compared with those in typical orbs which lack temporary spiral lines?
- Where do frame lines break when they are stressed this same way?
- Do the sites on radii where breaks occur in *Allocyclosa* correspond to the sites where break-and-reel began during radius construction (are possibly doubled portions of the radius less subject to breaking)?

A7. Orb damage in nature

- Do the kinds and amounts of damage that accumulate in the orbs of different species over the course of a day follow the same patterns (use repeated photos of the same webs)?
- Is it possible to repeat the unique observation of Smith (2006) of the orb of the Australian *Poltys* that disintegrated when the substate to which it was attached (twigs) was jarred?
- What is the relative importance in different species of the different advantages of secondary frame lines (save silk, stabilize primary frame, increase web extensibility) (make additional measurements like those in Fig. 3.27)?
- How do different species vary with respect to the minimum wind velocity needed to cause sticky spiral lines in the orb to adhere to radii or to each other?
- Is wind that is more nearly perpendicular to the plane of an orb less likely to produce damage through adhesions between lines (e.g., Fig. 10.4)?
- Are web renewal rates in species that built multiple webs/day species greater in smaller individuals (as thought by Craig 1989)?

A8. Stabilimenta

- Do gape-limited lizards show behavioral indications of reluctance to attack when presented with *Argiope* in combination with X stabilimenta, as supposed by Schoener & Spiller (1992)?

B. Non-orbs: designs, building behavior, cues

NOTE: Many of the same questions mentioned in other parts of this table can also be asked concerning non-orb webs such as funnel webs, the aerial sheets of linyphiids and theridiids, “substrate” webs such as those of filistatids or *Loxosceles* spp., etc. Similarly, many of the question asked in this section can be asked for many different types of non-orbs. Incredibly, even though nearly every house and garden in the temperate zone hosts agelenid and linyphiid spiders, and linyphiids and their allies constitute the most speciose groups of all spiders, there is neverthless not a single thorough, detailed study of the web building behavior of any species in these families (or, for that matter, of that of any non-orb builder).

B1. Phylogenetic patterns in the details of behavior

- Do the legs that hold the dragline and the line to which an attachment is being made provide useful tax characters in non-orb weavers?
- Do other web-building RTA species, in addition to the lycosid *Aglaoctenus*, utilize aerial bridge lines in web construction (it seemed to be absent in the pholcid *Modisimus*)?
- Do the legs of species that build dense sheets (e.g., *Nihonhimea tesselata* THD, the physoglenid *Physoglenes*, the diguetid *Diguetia canities*, and the psechrid *Psechrus* sp.) follow each other while the spider is in a sparse tangle, but cease to follow each other when she is walking on a dense sheet? Is there a phylogenetic pattern in these data?
- Do following legs of non-orb spiders make asymmetrical lateral short-distance searching movements (prolateral with I and II and retrolateral with III and IV)? Is there phylogenetic information in the distribution of these asymmetrical movements?
- Does sliding the tarsal claw IV along the dragline occur outside the group araneoids + deinopoids (i.e., is it a synapomorphy of this group)?
- Does sliding other tarsi along lines (e.g. *Nephila clavipes* radius construction – section O6.3.2.2) occur in any non-orb weavers?
- How widely is the ability to break and reel while walking under a horizontal line distributed taxonomically? Is this synapomorphy for araneoids?
- Are the leg movements used by different groups to climb draglines all the same? Is there phylogenetic signal in the differences?
- Are the differences in the forms in which cribellum puffs are molded correlated with different movements of the posterior median and lateral spinnerets in different taxa, and is there phylogenetic signal in the differences?

B2. Descriptive details of construction behavior

- How does construction behavior (stages, patterns of activity, details of how legs and spinnerets are used, whether legs follow each other) vary in different families (check for phylogenetic patterns) (use video recordings and Lamoral’s technique (1968) of marking early lines with magic markers)?
- Does the amount that legs are rotated increase when the leg seizes lines at smaller angles with its longitudinal axis? Is this true for all non-orb web spiders and all of their legs?
- Observe crucial details of the construction behavior of diplurid mygalomorphs that build elevated webs, such as *Diplura* and *Linothele* that are of special interest in understanding the evolution of aerial web: the legs used to walk along a single elevated line (sideways walking?); and how the spinnerets are used in attaching aerial lines to each other.
- Do groups that build dense sheet webs (e.g., zoropsid *Tengella radiata*, the pisaurid *Architis* sp., hahniids, etc.) use the same spinneret lifting behavior to spread the lines as a swath is being laid, as occurs in the diplurid, agelenid and lycosid species that have been observed?
- Do species that lack tartipores, such as the old “haplogyne” set of families, moult without being suspended from lines (as predicted by the supposed function of tartapores)?
- Are pholcid spiders able to adjust their web building behavior (especially fill-in behavior when building a sheet) and their attack behavior to compensate for loss of their legs IV? Can they learn to improve the effectiveness with which they use alternate legs?
- How do mygalomorphs use their claws to grasp the silk lining of their tunnels? Are the details variable, as in *Kukulcania hibernalis* (section 2.4.2)?
- How do species with 2 claws and claw tufts climb vertical draglines? How do salticids (with 2 claws and claw tufts) walk across orbs?
- How does male behavior in constructing sperm webs vary in different groups (especially mygalomorphs, liphistiids)? Are some behavior modules employed that also occur during web construction in these or other groups?
- Are there taxonomic patterns in the timing of orb construction during the day and night (use Table 8.2 as a starting point)?
- Do any non-orb species show handedness (bias toward one side or another) as seemed to occur in the austrochilid *Thaida peculiaris*) (Lopardo et al. 2004) (preliminary data on sticky spiral spacing in *Uloborus diversus* UL (WE) argued against handedness; but it might not be so disadvantageous in non-orb species)?
- Do spinneret movements (especially posterior lateral spinnerets) vary in different funnel-web construction contexts (e.g., exploration, spreading swaths, sheet fill-in behavior) in diplurids and agelenids? Do these movements differ in species with similar web designs but longer or shorter spinnerets?
- How widespread taxonomically is following behavior by different legs?
- How widespread taxonomically are one-sided and two-sided walking behavior along horizontal lines?

B3. Cues guiding construction

- Do non-orb weavers use some of the same sorts of cues to guide construction behavior as those used by orb weavers (could use simple techniques developed with orbs, such as breaking lines during construction, marking lines laid early during construction with a magic marker to be able to distinguish them later, and altering the form and properties of the supports available for the web) (*Frontinella pyramitela* (LINY) would be especially interesting, as the lines at the center of sheet are tighter - Suter 1984)?
- Can spiders that build webs around retreats (e.g. *Tengella, Agelena, Kukulcania,* etc) judge the hardness of the substrate in which there is a cavity, and if so, which cues to they use to make these distinctions (test with materials that spiders might find in nature)?

- What cues do theridiids use to choose a smooth substrate to which to attach their gumfoot lines (use direct observations of building behavior and experimental modifications of substrates: for instance, break all gumfoot lines, leaving the tangle above intact and then changing the substrate, thus standardizing the amount of tangle above)? Do gumfoot pholcids use the same cues?
- Which behavioral cues are used by groups like *Kukulcania, Liphistius, Uroctea,* and others whose webs are approximately radially symmetrical webs that allow the spider to add more or less equally to different sides of their webs during the sometimes prolonged period of construction (e.g., Fig. 5.11)? Similarly, how do they bias web repairs toward damaged or missing portions of the web (e.g., Fig. 7.49)? Do the spiders remember (perhaps using fixed points of reference)? Do they patrol the web (systematically or otherwise) to find empty sectors?
- What effect does altering the lyriform organs on legs on web designs and leg positions in non-orb spiders?
- How does experimental modification of tensions or removal of captured prey from the web affect subsequent repair behavior?
- Does removal of palps alter construction behavior in any way, or make it more difficult for the spider to release lines it has seized as it walks across a dense sheet (as Hingston 1920 observed in the lycosid *Hippasa*)? If so, what is the explanation of this unexpected effect?

B4. Web function and design
- What are the mechanical demands imposed by the environment on non-orb web designs in nature (document web damage in nature)?
- How does selection favoring stopping abilities and web visibility, to mention two, differ for different web types, as for instance linyphiid and agelenid sheet webs, filistatid and oecobiid substrate webs, and orb webs?
- Are prey sometimes snared by multiple gumfoot lines, and if so, does this correlate with greater capture success (placing sticky lines close to each other in such webs does not have the associated danger of adhesion to other other lines due to movements in the wind)?
- Are there environmental variables that correlate with the dramatic intra-specific variations in the presence and abundance of sticky lines in some linyphiids (Peters and Kovoor 1991) and theridiids (Eberhard et al. 2008*a*)?
- Are the holes ripped in sheets by the impacts of high energy objects greater or otherwise more serious in non-orb sheet webs (linyphiids, theridiids, etc.) when compared with holes ripped in the orb-like sheets of *Cyrtophora* (as predicted by arguments of Cranford et al. 2012 and Aoyanagi and Okumura 2010)?
- Do non-orbs differ with respect to the importance of capturing rare, large prey (section 4.2.2)? If so, do such differences correlate with differences in web design?

B5. Chemical and mechanical properties of silk
- Are there differences in the chemical composition of the tiny sticky droplets, such as those in the webs of linyphiids, *Synotaxus* spp. pholcids such as *Modismus guatuso,* and some theridiids such as *Anelosimus pacificus, Nihonhimea tesselata,* as compared with that of larger droplets on gumfoot lines of theridiids and the sticky spiral lines of araneioids? Do the differences help explain the puzzle of the seeming lack of a function for the tiny droplets?
- Does the chemical composition of the sticky silk on the gumfoot lines of pholcids (presumably derived from piriform attachment silk) differ from that on theridiid gumfoot lines (presumably derived from aggregate lines used in prey wrapping)?
- Are there correlations between the chemical composition and mechanical properties of the silk of spiders that build different types of webs (e.g., dense sheets, sparse sheets, tangles)?

B6. Test for cues used in web construction by studying attack behavior
- Do sheet weavers such as *N. tesselata*, pholcids, linyphiids return to the retreat or normal resting place following an attack on prey by using changes in tensions on some lines (as in *Frontinella pyramitela* – Suter 1984), visual cues from the environment (as in the agelenid *Agelena labyrinthica* (Görner 1986), gravity (in species with domed webs?), or path integration cues (as in *A. labyrinthica* - Görner 1986)?
- Does changing tensions on these webs (e.g. by bending wire supports) alter these spiders' abilities to return to their retreats? Does it change their construction behavior?
- Were the ancestral cues and responses to these cues that are used by non-orb spiders to guide construction behavior converted for use in orb construction; or did orb construct involve evolution of new abilities and responses?
- What determines what is done and which order when a theridiid spider raises her retreat from the ground to suspend it in a tangle (repeat and expand the observations of Freisling 1961)? Are any of these cues and the responses to them used in web construction?
- Do theridiids wrap prey that have longer projections such as legs or wings more than others, as in like araneids and uloborids (add or substract projections of the prey)?
- Can theridiids, linyphiids, or other species with aerial webs orient correctly to prey that are completely immobile, using web shaking to find them? Does web shaking occur in species with webs close to the substrate?
- Is the apparent correlation in *Kukulcania* (not biting the head and having a web with strong retention abilities) present in other groups?

B7. Others
- Does the presence of an egg sac or a retreat increase the chances that theridiids will build a web (or will stay in given support)? If so, what are the stimuli from the sac or retreat that influence the spider's behavior?
- What are the cues that theridiids, diguetids and other spiders (including araneids) use to select small objects such as pieces of paper or leaves or other detritus (from under the web?) that they use to make aerial retreats? How do these cues differ in different taxonomic groups (which have probably evolved retreat construction independently)?

B8. Test the function of tangles as protection from predators
- Among linyphiids that build tangles under the sheet, is the spider more likely to sit in the center of the web rather than at the edge (as predicted)?

- Among linyphiids that lack tangles, is resting off the edge of the sheet under a supporting object more common (as predicted)?
- Is the spider more likely to sit in the center of the web rather than at the edge than in linyphiid species that build tangles under the sheet as opposed to species lacking tangles (as predicted by the predator defense hypothesis)?

B9. Ecology

- Does lack of appropriate retreats limit populations of species such as segestriids, agelenids, filistatids, *Loxosceles*, *Tengella* (set out lots of artificial retreats that have appropriate sizes and designs for particular species, and check whether populations become more dense)?
- Do aspects of the substrate near a retreat influence web size and design in such species? Is the extreme flexibility in *Tengella radiata* (Fig. 10.7) typical of other groups?

B10. *Fecenia, Titanoeca, Badumna*

- Do any of the uniformities between araneoids and uloborids in the cues used to direct orb web construction and responses to these cues (see Table 10.3) also occur in spiders that construct pseudo-orbs (if the cues and responses are similar, then construction constraints *sensu* Coddington 1986b are likely to explain them, given the high likelihood that the pseudo-orbs in this group evolved independently; the arguments adduced by Eberhard and Barrantes (2015) favoring orb monophyly would be weakened)?

B11. Wasp-spider interactions

- Is it possible to replicate the observation of *Anelosimus* sp. near *eximius* under the influence of *Zatypota* sp. nr. *solani* (Eberhard 2010) using the leaves of a plant to form part of the chamber formed by the cocoon web?

C. Orbs: Building behavior

C1. Taxonomic patterns

- How much does the site where the spider breaks the provisional radius on the way back to the hub during radius construction vary in different groups? Are there phylogenetic patterns in this site (*Zilla diodia* broke the line nearer the hub – Zschokke 2000b)? Does the site vary with the length or the orientation of the radius?
- Do uloborids differ from other orb weavers in having a greater tendency to circle the entire web very early in stsp construction?
- In what sequence are the parts of the deviant “purse” webs of the Tasmanian araneid *Paraplectanoides crassipes* (Fig. 10.28) built? Does their construction behavior show any vestiges of orb web construction?
- In what sequence are the parts of the “quilt” webs of the Tasmanian anapid *Tasmanapis strahan* (Fig. 10.27) built (is each orb built as a unit)?
- Do the details of hub removal behavior (and subsequent filling in) vary among taxonomic groups of araneoids (possible comparisions include the wide hole of *Micrathena* vs. the smaller holes of *Chrysso* and *Leucauge*, or sewing up tiny hole at the center by *Cyclosa* vs. closure of a wide hole by *Argiope*)?
- Does the number of times legs IV pull additional sticky spiral line between attachments vary with phylogenetic relationships (do tetragnathids ever do this)? With orb designs?
- How much do the different legs rotate when they seize lines at different angles (in all cases expect less when the line is more nearly perpendicular to the leg)? Does this rotation vary in different taxonomic groups?

C2. Variations in behavior and their consequences

C2a Sticky spiral

- How much does variation in the sites grasped by oIII and oIV with respect to the inner loop during sticky spiral construction correlate with variations in the site where the spinnerets make the attachment (use large) species like *Nephila clavipes* and *Argiope argentata*)?
- How do the legs and palps move when the temporary spiral is broken during sticky spiral construction (use large species like *Eriophora* or *Argiope*)?
- Is there a correlation between the positions of oII and oIII steps as move outward on radius at the moment when oI touches the inner loop in *Zosis geniculata* (for instance, when oIII has already started its step outward (hand over hand with lII) at the moment that oI touches the inner loop and the sticky spiral space that is produced (when the III’s is step shortened is the sticky spiral space smaller) (videos)?
- What are the metabolic costs of combing out cribellum silk for a uloborid as compared with producing dry lines, or with producing araneid sticky spiral lines? In general, what are the metabolic costs of different stages of orb construction (measure with a respirometer)?
- Does the number of times that legs IV pull additional sticky spiral line between one attachment and the next vary with orb designs (are there more pulls when the radii are farther apart)?
- Is there any correlation between the slant of an orb and the precision of building behavior (especially sticky spiral spacing) (does lack dexterity produce some variation)? Does a species the builds more or less horizontal orbs (e.g., *L. mariana*) become less precise when the web is placed in a vertical orientation during sticky spiral construction (are perfectly vertical orbs more difficult to build)?
- Is there any relation between the precision of sticky spiral spacing and the speed with which the spider makes attachments in different parts of the web (especially when the spider is climbing rather than descending in a vertical web) (especially easy in Micrathena where spiders seldom turn back during stick spiral construction)?
- Does removal of palps in an orb weaver affect the removal of temporary spiral lines during sticky spiral construction?
- Do stubby-legged species reel in r_n while holding the temporary spiral and just before attaching the sticky spiral more often than long-legged species?

C2b Temporary spiral and hub

- Are there errors by legs oI and oII during hub loop construction, such as occasional failures to grasp the correct radius (video recordings)?
- When the outer loop of the temporary spiral is broken during sticky spiral construction, does the frequency with which the spider taps toward sites where lines were "expected" to occur increase?
- Is the behavior used to make false hub repairs in *U. diversus* (Fig. 6.18) or others similar in any way to the building behavior of pseudo-orbs like those of *Fecenia* or *Titanoeca*?
- Are the sizes of the zig-zags in adjacent radii that are produced by the same segment of hub spiral greater in longer radii (perhaps due to increased extensibility with length, or to lower tensions)?

C2c Radius construction

- Are there more searching movements with legs I (searching for an open sector) preceding the radii that are laid later in the radius construction stage (when open sectors are less easily sensed)?
- During radius construction, does the site where the spider breaks the provisional radius while she is returning to the hub vary in ways that would increase the web's resistance to prey impacts (break farther from frame in smaller species with weaker lines; above rather than below the hub; farther from the hub with longer radii)?
- Is there ever any attachment at the point in araneids or tetragnathids where the provisional radius was broken and replaced with the definitive radius at the start of cut and reel behavior? (Zschokke 2000b found no attachments in *Zilla diodia*)?
- Are there variables that correlate with the exceptions made to the "alternate sides" pattern of radius construction?
- Do all araneids and tetragnathids fail to attach the definitive radius to the provisional radius just before breaking the provisional radius, and thus fail to take mechanical advantage of the provisional radius (as in *Zilla diodia* – Zschokke 2000b)?

C2d Exploration

- Does the speed of walking increase when the tension on a horizontal line is greater? Is this associated with changes in exploratory behavior of the legs?

C2e Others

- How are legs rotated during different activities (place small marks on the legs of a large species such as *Nephila*, *Eriophora* or *Fecenia* and then check for rotation as the spider walks and searches for, seizes, and then releases lines that make different angles with the leg)? Are rotations similar in non-orb building species?
- Does the degree of planarity of an orb increase in a species when the orb is more nearly perfectly vertical (it may be more difficult to make a pefectly planar orb when it is horizontal than when it is vertical)?
- What effects (if any) will repeating the Vollrath experiment (removal of leg I in the penultimate instar to create spiders with one leg of a pair shorter than the other) for legs II, III and IV have on the web design?
- Do species that build perfectly vertical webs have special behavior to avoid contacting or otherwise becoming entangled in the lines that are directly below them when they are building new radii, temporary spiral, or sticky spiral?
- What are the metabolic expenditures while waiting at the hub, and how much do they increase in species that hold their webs taut?
- Is the spider more "alert" (responsive to prey stimuli) and more active (expending more energy) soon after web construction than several hours later (must separate diurnal rhythms from changes associated with web *per se*)?
- How imprecise are the usual typological designations of "the" orb construction behavior in different taxonomic groups? For instance, how often does the spider actually fail to touch the inner loop during inner loop localization behavior? Will the existence of variations of this sort ("errors"?) in some behavior patterns but not others help understand how behavior has evolved?
- Do different individuals have different styles of web design (as suggested by Witt et al. 1968)? Are there suites of individual differences that fit together into adaptive modes (e.g. alternative phenotypes) (or are the variations non-adaptive, as in Sih's "personalities")?
- How much of the intra-specific variation in orb web designs is due to genetic differences (could use classic techniques such as controlled genetic crosses, comparisons of the web designs in the offspring from different crosses, and artificial selection on different web traits could information on the potential to evolve in different directions in different traits)?
- Does the degree of compensation for leg loss in orb construction behavior vary taxonomically (the prediction would be that species which more often lose legs (*Nephila*) compensate more effectively than those that seldom or never lose them (*Leucauge mariana*)?
- Is it possible to induce "senile" webs in *Uloborus* by manipulating feeding or humidity or water or mating or oviposition)?

C3. Effects of CNS and miniaturization

– Are the responses to Hingston experiments as consistent in tiny as in large spiders? (second instars vs adults of *Nephila clavipes*) (is miniaturization associated with reduced precision of response)?
- Can tiny spiders (and other animals) clean their legs as efficiently and effectively as larger individuals? Can they compensate equally well for missing legs when they clean themselves?
- Which parts of the leg IV ganglion in *Nephila* are relatively larger compared with those of other araneoids that use legs I in inner loop localization?
- Do parts of this ganglion become reduced, and parts of the leg III ganglion become enlarged when leg IV is lost (use ganglia on the other side as controls)?

C4. Use wasp chemicals to elucidate control of building behavior

- Can the identities of the chemicals used by parasitoid polysphinctine wasp larvae to manipulate their hosts' web construction behavior be determined by using the timing of gene expression, the identities of these gene products (neurotransmitters?)?

- Can the functions of different sites in the spider's CNS be inferred by determining where in the CNS these wasp products accumulate, and where products accumulate in species in which different aspects of construction behavior are affected?

D. Cues guiding orb construction (and removal)

D1. Cues that direct orb construction

D1a. Sticky spiral

D1a1. Tensions on radii (and related stimuli)

- If the tensions on pairs of radii are reduced slightly (by breaking lines at the center of the hub, by breaking secondary frame lines, or by breaking temporary spirals in *N. clavipes* webs), is there any effect on the spaces between sticky spiral loops (perhaps it is more reasonable to expect that smaller, more biologically realistic changes in tension such as these, rather than the large changes produced by breaking the radii in previous experiments such as Fig. 7.15, will have effects)?
- Is it possible to elicit zig-zag double attachments of the sticky spiral in uloborids by altering web tensions (if zig-zag attachments are more common on longer radii, and if radius length is sensed by extensibility, then an increase in zig-zags would result from lower tensions)?
- Will Hingston's experiment (break the inner loop of sticky spiral) produce the same changes in sticky spiral spacing when it is performed on when r_n is lax (broken farther in) (this constitutes a further test of the importance of distances rather than tension-dependent cues) (do with *L. mariana* because control data already taken)?
- Does changing the tensions on lines by moving supports for anchor lines at different stages of construction alter construction behavior in any way (also exploration, radius, temporary spiral construction)?

D1a2. Other stimuli guiding sticky spiral placement

- Do variations in small behavioral details (such as positions of legs when first makes contact with the inner loop) correlate with variations in responses in Hingston experiments (use in large species such as *Argiope* or *Eriophora*)?
- Will experimental addition of "barrier lines" of sticky silk (from collapsed sectors of other webs) elicit Joe Morgan responses? Is it possible to induce the spider to "break the rule" when the angles that these experimental lines make with the spider's path are too sharp?
- If both a single loop of temporary spiral and the inner loop of sticky spiral are broken experimentally (e.g., the Hingston experiment), is the response to the Hingston experiment reduced (as predicted)? Does one stimulus sometimes prevail over the other?
- Does the spacing between adjacent puffs of cribellum silk get wider near the end of the sticky spiral line laid on the first day in "2 day webs" of *Z. geniculata*? Are they smaller in the first portions of sticky spiral laid the second day (see Fig. 7.20)? (both might occur if the spider was running out of silk at the end of the first day)?
- Are there special sensory structures at the sites on the legs that contact sticky lines when they are used in inner loop localization behavior (on the ventral surface of I in araneids, on the dorsal surface of I in tetragnathids, on the dorsal surface of IV in *Nephila* spp. and *Micrathena duodecimspinosa*). What happens when these sites are covered (e.g. with superglue)?
- Do variations in responses to Peters' experiments to test his "sector" hypothesis (break radii to increase distance between them and thereby increase sticky spiral spacing) (Fig. 7.14) correlate with differences in positions in the web (above/below; the distance to the outermost loop of temporary spiral)?
- Will direct observations of sticky spiral construction by spiders in which one leg I is shorter than the other confirm Vollrath's conclusion (1987) from indirect evidence that the spacing is reduced when the shorter leg I is the outer leg, but not when the longer leg I is the outer leg?

D1b. Hub and temporary spiral

- Is the temporary spiral spacing altered in spiders in which one leg I is shorter than the other (repeat Vollrath experiment of removing one leg I in penultimate nymph)?
- If the tensions on alternate radii are reduced by breaking them near the hub during temporary spiral construction, are the zig-zag connections of temporary spiral attachments larger on the lax radii in *Nephila*?
- What variables affect the precision of *Nephila* during temporary spiral construction (frequency of mistaken attachments of radii to each other)?
- If the tensions on radii are reduced experimentally during hub construction (e.g., break secondary frame lines), will the spider be induced to make double attachments of the hub spiral and temporary spiral, and will the zig-zags at these attachments be larger?
- If the temporary spiral is experimentally eliminated just after it is finished, does the spider build another, and is the second one smaller than the first (as in the Peters experiment with *Araneus diadematus*) (which had a sample size of N=1)?
- If some radii are broken just as hub loop construction begins, will the number of hub loops be reduced (do the cues responsible for the correlation between number of hub loops and number of radii involve the spacing between radii that the spider encounters while she builds the hub)?

D1b. Radii

- Are false starts in radius construction (section O6.3.2.1) biased (with respect to radius length, inter-radius angle, later filling of same hole, the angle of the radius with gravity)?
- Does the spider adjust the distance she moves along the frame line during radius construction on the basis of the angle with the frame when she goes around a corner at the end of a frame line?
- When radii are repeatedly broken during radius construction (as in the experiment of Reed 1969), does the spider's behavior prior to laying each new radius gradually change (any sign of "frustration"?)? Does the precision with which the replacement radius is laid (inter-radial angle) correlate with this behavior? Do any variables (the site at which the preceding radius was laid? length of pause at hub?) correlate with variations in the attachment sites when radii are repeatedly broken and replaced in this experiment)?

- Do other araneids or tetragnathids attach the definitive radius to the provisional radius just before they break the provisional radius during radius construction (in contrast with *Zilla diodia* – Zschokke 2000b), and thus take mechanical advantage of the provisional radius? If so, is there any bias in which radii are attached this way?
- If a spider is induced to build a replacement orb that is smaller but uses the same frame lines (e.g., spray with water after photo), does the number of radii go down despite total radius length being the same (expected if number of radii is determined by number of sticky spiral loops; not expected if determined by area of the orb)?
- Will other species give the same results when radii are broken experimentally during radius construction as Reed 1969 observed with *Araneus diadematus*? What variables affect the precision of the choice of an attachment site when radii are broken and replaced (does it gradually decrease as radii are broken repeatedly)? Do noise and lights break concentration?
- In photos of orbs in which it is possible to deduce the order of radii laid (e.g. *Uloborus*), did the spider correct this distance she moves along the frame when she went around a corner (compare with *M. duodecimspinosa*)?

D1c. Others (exploration, etc.)

- If the flexibility of a support is increased experimentally while the spider is early in construction (as in the Tilquin 1942 experiment of removing a stiff rod from a more flexible material) does the spider adjust cut or tighten lines in response?
- If the tensions on lines are altered by moving supports at different stages of construction, which aspects of the orb's design are altered?
- Will experimental reduction in the barometric pressure induce the spider to perform snow-plow web removal when the web is loaded (with powder (as in WE observation of *Leucauge venusta*)?
- What is the effect (if any) of adding disturbing objects in the web plane during exploration behavior to replace a first web that was destroyed (see also G2 below)?
- Does the angle of the cone correlate inversely with the area of the web in *Anapisona simoni*? With the vertical space available for attachments?
- Do larger orbs correlate with higher temperatures, as observed in *Argiope keyserlingi* by Blamires et al. 2007?
- Is hub removal behavior altered if the hub spiral lines are broken experimentally during sticky spiral construction? If so, selective breakage reveal which cues are used by the spider to guide removal behavior?
- Do other *Cyclosa* species repair their orbs in the way described for *Cyclosa confusa* by Shinkai 1998? if so, how do the spiders orient themselves?
- What effect does inactivating the lyriform organs on legs have on web designs? Do the same sorts of alterations that affected dead reckoning abilities in *Cupiennius* (Seyfarth & Barth 1972) alter web designs in orb weavers (especially web traits that are likely to be affected by exploration behavior)?
- Does another experimental alteration that may affect the spider's sensation of how far she has walked (remove the accessory setae from her tarsi, making it harder for her to grasp lines and thus causing her to slip on them) alter the same aspects of orb design?
- Is the orb design altered if the sense organs at articulation of the abdomen (Agnarsson et al. 2008) are modified?

D2. Learning

- Can species that normally build vertical orbs be induced to build horizontal orbs, as occurred in *Argiope argentata* (da Cunha and Ades 2012)? If so, does the ability to adjust to horizontal improve with practice, as also occurred with *A. argentata*, and which specific behavior patterns changed?
- Does compensation for leg loss in web construction or prey wrapping by orb weavers improve gradually (as would occur with learning), or are the changes immediate and automatic?
- Is the degree of flexibility in adjusting to loss of a leg correlated with the frequency of leg loss in the field in different species (as expected if the ability to make adjustments is innately programmed)?
- Can spiders learn that a given support is less stable (experimentally displace it toward the hub to make an anchor line go slack), and subsequently avoid others with similar cues even though they are stable (use paper strips)?
- Will more complete experiments concerning the effect of prey location in the web confirm that the size of the sector where prey was captured previously is enlarged in subsequent orbs (Heiling 2004)?

D3. Etc.

- Does the decision to reingest an old web correlate with poor feeding history in groups such as *Zosis* or *Uloborus*, in which silk recycling is inconsistent?
- If a radius is broken just before stabilimentum construction (e.g., in *Uloborus diversus*), does the increase in the tension on the two adjacent radii (and thus the decreases in their extensibilities) increase the chances that a stabilimentum arm will be placed on them (predicted by the hypothesis of Eberhard 1973 that spiders chose radii on basis of tension or extensibility)?

- Will experimental reduction in the barometric pressure induce orb weavers to perform snow-plow web removal (Carico 1986) when the web is loaded with powder (as occurred in one *Leucauge venusta*) (WE)? Will a sudden decrease in temperature potentiate this response?

E. Ecology and interactions with prey

Note: *Araneus diadematus*, the white rat of lab studies of web design and building behavior, seems to have almost never been studied in the field, and would be a preferred species for many of the topics below. Many of the same questions should also be asked of species with non-orb webs, such as funnel webs, the aerial sheets of linyphiids and theridiids, "substrate" webs such as those of filistatids and *Loxosceles* spp., etc.

E1. Website choices

- What behaviors characterize preferred vs. non-preferred websites if pairs of possible websites are offered in captivity (place the spider on a silk line between the sites to guarantee equal access to both at the beginning of the presentation)?
- Do species whose webs are more expensive spend more time in discriminating among possible web sites? Do they make fewer mistakes (e.g., build at sites that are too small or otherwise unappropriate?
- Do species with a short time window for web construction (e.g. dusk – late enough to avoid predators, early enough to catch peak of insects in the air) (e.g., *Metazygia gregalis*) explore less thoroughly, and make more mistakes in judging websites?
- Do species that prefer rigid supports utilize chemical cues, (e.g. leaves vs. twigs, etc.), movements of the substrates themselves, or some other cues to distinguish stiff or stable as opposed to flexible or unstable substrates from each other? Can they (both orb-weavers and non-orb weavers) learn which support is less reliable (use experimental displacements of suppports toward the web to make it go slack), and subsequently avoid it?
- Do the specific sites that are occupied vary from year to year (certainly true)? Can field sites be made stable enough to argue that such variation supports the idea that web sites are not limiting?
- Does the presence of egg sacs or a retreat increase the chances of web construction in species such *Cyclosa/Allocyclosa, Philoponella* spp., *Nihonhimea tesselata, Theridium evexum,* etc.)?
- Are nocturnal orb weavers are attracted to lights at night (as suggested but not demonstrated by some experiments – see section 8.4.3.2.5), or do they just gradually accumulate near lights as a result of not moving away because of improved prey capture?
- Will replication of the Heiling 1999 study to test for a preference to build at lighted sites (in a cage) in a more biologically contexts or with a different species that occurs near lights (e.g., *Metazygia* spp.) give the same results (see section 8.4.3.2.5)?
- Does rain damage induce spiders to leave websites in the field (could put transparent umbrellas over some webs, or spray some with artificial rain)?
- How does prey capture vary when spiders that have been induced to build orbs in portable hoops or frames are placed in different sub-habitats in the field? Experiments of this sort could help solve the vexed problem of measuring habitat "quality" in terms of "available" prey (sections 3.2.5.4, O3.2.3). Experimental pairing of these frames with prey captured by nearby spiders in natural webs could test the effects of the frame itself.
- Are preference for certain types of substrate (e.g. dead over living stems in *Eustala* spp in Brazil, *Metazygia* spp.), *Acacia* trees (with *Pseudomyrmex* ants) in *Eustala illicita*, *Piper obliquum* plants (with *Pheidole bicornis* ants) in *Dipoena banksi* (THD), wood over stone in *Larinioides sclopetarius*) guided by chemical to cues? If not, what other cues are used?
- Are spiders able to sense the degree to which a site is sheltered from rain (or other hostile forces such as wind), and choose web sites accordingly?
- How do spiders determine the height of the web above the ground? Some groups clearly prefer websites near the ground (*Argiope, Gea, Pronous, Uloborus diversus, Anapisona simoni*) while others just as surely prefer high sites (*Gasteracantha, Hypognatha, Bertrana*). If individuals of a "low" group are placed high up (e.g., in standardized cages which can be designed to provide some but not other stimuli like light, wind, humidity, etc. from the environment), are they less likely to build?
- Do species with more strict requirements for retreats (cavities, etc.) respond less readily to reduced prey capture as a cue for abandoning a website (as in *Seothyra henscheli*)?
- Does the number of available retreats limit population densities in species such as segestriids, agelenids, filistatids, *Loxosceles*, *Tengella* (set out lots of artificial retreats that have appropriate sizes and designs for particular species, and see if populations become more dense) (extend the dictynid study of Smith et al. 2016)?
- Are more poorly fed individuals more likely to build in sites that are only sometimes acceptable?
- Do spiders avoid windier sites when given the choice? Does this differ with species?
- How do variables related to website (size and shape of space) interact with variables related to retreat characteritics (degree of protection, size, site) in orb weavers such as *Zygiella x-notata, Eustala illicita,* and *Chrysometa* spp.?
- How much do traits of the substrate in which sheltered retreats occur influence web size and design (as in *Kukulcania hibernalis*)? Is the extreme flexibility in the zoropsid *Tengella radiata* (Fig. 10.7) typical of other species?
- Do sites on the lee sides near the tops of ridges where there is a prevailing wind have especially abundant populations of web-building spiders (as seems to be the case at several sites in Costa Rica and Panama) (this would argue in favor of prey limitation of population sizes)?
- Does the distribution of host webs (clustered/isolated) such as *Tengella, Kapogea, Metabus, Tidarren* affect their populations of commensal and kleptoparasitic spiders (e.g., *Argyrodes*) as was found in *Nephila clavipes* by Agnarsson 2003)?
- Do playbacks of the sound of buzzing flies induce spiders to build webs?
- Are orb planes aligned with the wind at field sites where there is a strong prevailing wind. If so (as occurs in some – see Hieber 1984), is this due to unequal rates of destruction or to biased construction behavior?

E2. Prey behavior - attraction and retention

- Are the retention times for the same prey lower nearer the hub? Are they especially small very near the hub (thus explaining why free zones exist)? Are they especially small nearer the edge (wider spacing sticky and radial lines)?

- If the tensions on an orb are reduced (by bending a flexible frame), do the retention times decrease? Do retention times increase if the web is tensed?
- How much does the degree of sagging vary with different lengths of stsp segment and different wind velocities (video recordings)?
- Can lab experiments confirm the possibility that nocturnal webs are visible to insects (especially moths?) and are avoided (Craig 2003) or attracted (Lai et al. 2017) (use infra-red recordings of prey behavior)?
- What are the effects of wind on prey velocities and directions, and how do they influence the abilities of orbs to stop prey (include wind stress as well as prey stress)?
- Do the impacts of falling objects rupture horizontal orbs less often when when there is an upward wind (high speed video recordings) (this would test likely effects of horizontal wind on vertical orbs)?
- Do prey alter their struggling behavior on the basis of the numbers of lines that contact their bodies, the sites where the lines make contact, or the ease with which they break adhesion to the lines?
- Does retention in different types of webs (orb vs. tangle, strong vs. weak lines) elicit different types of escape behaviors from the same insect species? Do different types of prey utilize different escape strategies?
- Do prey respond to the vibrations produced by spiders, such as web jerks, or vibrations as approach just before the spider attacks?
- Do different types of prey utilize different escape strategies?
- Will sticky line traps (e.g., Lubin and Dorugl 1982) capture the same mix of moths as *Cyrtarachne* spp. and related genera when placed in the same habitat at the same hours of night (and thus explain their puzlzing apparent strong specialization on moths)?

E3. Web dynamics in the field

- Do the damage repairs that spiders make in their webs improve web durability in the field? Do these effects vary in different species?
- Is it true, as speculated by (Craig 1987a), that flimsier webs of species like *Epilineutes, Leucauge globosa* suffer more frequent major damage in the field than the stronger webs of *Micrathena schreibersi*? Induce spiders to build in frames and move them between sub-habitats to check for website effects as well as web design effects.
- Is the relation between the size of the damage to the web and the chances that the spider will abandon a web site linear? Does the curve level off for especially small or especially large damages?
- What are the frequencies of different types of damage in the field (controlled experiments can probably allow recognition of the patterns of damage produced by different factors such as billowing in the wind (Fig. 10.4), swinging of individual sticky lines (Fig. 3.18), and tracks produced by the spider herself (Fig. 4.19)?
- How rapidly do different types of damage accumulate during the day in horizontal webs (e.g., *Leucauge*) and vertical webs (*Allocyclosa, Micrathena*)?
- Does the size of the anchor line (span of the orb) correlate with rate of accumulate damage?
- Can spiders predict the length of interludes in foggy or drizzly weather?
- Is the frequency of web construction inhibited by wind? By light at night?
- Do spiders like *Leucauge* (I guess yes), *Mangora* (I guess no), and *Uloborus* (I guess no) tend to build their webs near the upper edge of the herb layer in sites where the upper edge can be distinguished (e.g., palm grove)? Are the webs of younger nymphs built farther below the top of the herb layer?
- Remove spiders repeatedly from the same small plots, and map the sites that are colonized for species which move a great deal (e.g. *Mysmena*). Are the same websites recolonized over and over?
- Are there consistent changes in ecology during ontogeny re. prey sizes, prey velocities, web durability (Craig's hypothesis), sub-habitats of websites, website tenacity, or predation rates and predator species, and are there concomitant changes in web designs? Are there cases of lack of ontogenetic changes even though ecological pressures changed?

E4. Predators

- Which are the major predators in the field of different web-building species, and how do they find and attack their prey (a huge, difficult, and nearly vacant field - perhaps start with simple settings such as caves)?

F. Attack behavior and interactions with prey and predators

F1. Attack behavior, and associations with orb designs

F1a. Jerking at the hub

- Does jerking behavior by the spider at the hub increase the time that prey are retained in the web? Does it cause prey to fall out more quickly? Do the effects vary when the web is vertical rather than horizontal? If the web is loosened (e.g., by removing the center of the hub), do jerks more often entangle prey?
- Is jerking more common when the prey is larger? Is it more frequent when the prey is motionless?
- Are the sharp jerks of radial lines that often precede attacks more common for immobile than for struggling prey? For larger as opposed to smaller prey?
- Do these jerks further entangle prey (as supposed by some), or do they more liberate prey (as surely occurs sometimes)?

F1b. Speed and precision of response and attack

- In species in which the degree of vertical asymmetry of orbs is related to the spider's body size (presumably because larger individuals are increasingly slow in attacking prey above the hub), several predicitions can be tested: 1) Does the relative speed of attack upward (vs. downward) gradually decrease as spider gets larger? 2) Do the orbs of species with shorter legs relative to their body size (that do not run to reach the prey rapidly) (e.g., *Gasteracantha, Epeirotypus*) fail to show this ontogenetic trend in web design? 2) Are short-legged species more

likely to jerk, or to jerk for longer periods? 3) Is this ontogenetic change absent in species (both long- and short-legged) with more or less horizontal orbs?
- Do experimental manipulations of the hub (breaking radii, widening the hub hole, breaking radii held by III and IV) affect the speed or the accuracy with which the spider turns at the hub to initiate attacks on prey (use videos)?
- Do species with horizontal webs respond more rapidly or frequently to prey in front than behind the spider (as appears to be the case with *Leucauge mariana*) (this is likely to be especially interesting, because increasing the weight of the prey behind the spiders did not improve the responses, so the difference seems to be a question of attention, not stimuli from prey)?
- Do spiders with more vertical respond more rapidly and frequently to prey in different directions (e.g., better below than above the hub)?
- Is there a relation between ontogenetic allometry of legs in adult and early instars of different species and differences in attack speeds?
- Do the speed or accuracy of the turns to face toward prey vary with the site in the web (in front, behind, to side)? Is either of these variables associated with differences in orb designs (e.g. radius length)?
- If the degree of vertical asymmetry of orbs is related to the spider's body size (expected if attacks on prey above the hub by larger individuals are relatively slower), then several predictions can be tested: 1) does speed of attack upward vs. downward gradually decrease as spider gets larger? 2) Do the orbs of species with shorter legs (e.g., that cannot attack rapidly) fail to show this ontogenetic trend? Are these species more likely to jerk, or to jerk for longer periods? 3) Is this ontogenetic change absent in long-legged species with more or less horizontal orbs?
- Does *Nephila* consistently take the right path where radii split when attacking a prey (test on parts of the web to the side of the hub)

F1c. Types of attacks

- Can masking sense organs on leg I and II alter the bias toward "embrace and bite" rather than wrap attacks on lepidopterans by *Argiope argentata* - Robinson 1969)? Will it alter the especially cautious approaches to more dangerous prey such as vespid wasps?
- Do differences in attack behavior correlate with differences in morphology such as leg length across a wide spectrum of web spiders (see Olive for a sample of 2 species)?
- Is attack wrapping behavior (wrapping duration, wrapping site, length of the bite, number of bites, site bitten, time to reach prey, start to wrap before releasing the prey in *Nephila*) altered when prey are modified (e.g., add weights, remove wings, remove legs, remove scales)?
- Was Hington correct (1922c) that *Nephila* preferentially bites the thorax of large prey? If so, how does the spider find the head? Do other species show the same bias?

F1d. Learning

- Do attack strategies improve with repeated exposure to difficult prey (e.g., I. Escalante on the pholcid *Physocyclus globosus*)?
- Do individual spiders of the same species have "personalities" (timid, aggressive, duration of wrapping) in attacks on standardized prey? Do such individual biases correlate with previous experiences with dangerous or non-dangerous prey? Do they correlate with assays for "boldness" such as defensive responses to puffs of air?

F1e. Etc.

- Are attacks when the radius is attached directly to the substrate (and thus resonates more) less precisely oriented (as might be predicted from the discussion of Landolfa and Barth (1996)?
- Which of the several different aspects of attack behavior (speed of the turn at the hub, delay in beginning to move toward the prey after turning, the number of jerks before beginning to leave the hub, the number of jerks along the way, the speed of movement from hub to touch prey, the number of touches on the prey before initiating bite or wrap, the use of bite rather than wrap attacks) vary in accord with traits of prey? With the species of spider? Which traits of the prey (weight, long-leggedness, amplitude of vibrations, surface smell/texture, presence/absence of lepidopteran scales) elicit which variations (extend the studies of Robinson and colleagues with respect to variables and species)?
- Are pendulum returns (which must be somewhat costly due to need to climb line) more likely when webs are more nearly vertical (when tracks made in attacks are larger)?
- Can masking sense organs on leg I and II alter the special treatment that some prey receive (embrace rather than bite lepidopterans (as suggested by the observations of Robinson and colleagues); especially cautious approaches to vespid wasps or ants)?
- Do differences between species in attack behavior correlate with differences in morphology such as leg length?

F2. Prey behavior

F2a Behavior prior to contact with the web

- Do details of the behavior of potential prey insects in the vicinity of orbs in nature, such as their typical velocities, the directions they move with respect to both the web plane and horizontal, and their abilities to learn to avoid webs, vary in different species of spiders in ways the illuminate their choice of web designs? are all potentially important in understanding spider web evolution (e.g., compare species within vs above the herb layer, against solid surfaces such as tree trunks, leaves)?
- Does the context in which prey fly into webs (when frightened, during normal flight) correlate with their ability to avoid webs, to become less severely entangled, or to utilize different escape tactics (place orbs near sites with many prey of certain species, such as rotting fruit, cow dung, and then watch flies that encounter the web on their own and when they are frightened into the web)?
- Do insects adopt particular behaviors when they sense an approaching orb, such as speeding up to break through the web, or turning back sharply (extend observations of Craig to other species)? Do differences in prey behavior correlate with body size/compactness/typical flight velocity of insect as expected?

- Which species of prey of *Metabus* fly the late in the afternoon (when building behavior peaks)? Are they likely to produce less stressful impacts with orbs than those at other hours (as predicted by Buskirk's observation of less dense webs)?
- Can it be demonstrated that that nocturnal orbs are visible to insects and are avoided (as supposed by Craig 2003) (use infra-red recordings of prey behavior in captivity)?
- Does flying with extended legs reduce the chances of entanglement in webs in insects such as mosquitoes, *Drosophila* and sepsid flies (cut them off, glue to body, etc. and test with webs)?

F2b Escape behavior after impact

- Do prey species differ with respect to their escape behaviors (wing cleaning, leg cleaning, playing dead) (extend observations of Suter 1978 to other insects)?
- What are the mechanical events and escape behavior patterns that actually lead up to a prey escaping?
- Does prey escape behavior vary in horizontal vs. vertical orbs? Are some types of movements (e.g. wing vibration) postponed until other structures are free? Does the number of lines contacting the insect influence its escape behavior? Do different insect groups vary with respect to their tendency to "play dead"?
- Does the escape behavior of an insect change (become more violent) when the spider responds to it (jerks the web, begins to move toward it)?
- Are retention times especially small very near the hub (standardized prey), thus perhaps explaining why free zones exist?
- Are they especially small near the outer edge where the spaces sticky and radial lines are larger (film webs held near accumulations of sepsid or drosophilid flies that are disturbed)?
- If the tensions on an orb are reduced (by bending a flexible frame), do the retention times decrease? Do retention times increase if the web is tensed?
- Does alteration of prey properties, such as shortening or removing the wings or removing legs, induce changes in spider attack behavior (biting vs wrapping attacks, wrapping duration, wrapping site, duration of the first, long bite, number of bites, the site on the prey that is bitten, the time to reach the prey)?

F3. Feeding behavior

- When an orb-weaver rotates newly captured of prey at her mouth, does she tend to stop rotating and begin to feed at particular sites?. If the prey is bleeding from a hole, does this induce the spider to stop rotating and start to feed there?
- Is the pause between wrapping and beginning to wet the prey longer for larger prey in uloborids?
- Is the amount of wrapping determined by coat already applied (switch prey with different amounts of wrapping between spiders)?

F4. Predator behavior

- Do gape-limited lizards show any behavioral indications of greater reluctance to attack when presented with *Argiope* in combination with an "X" stabilimenta (as would be supposed by Schoener & Spiller 1992)?
- What are the major predators in nature, and of how does the behavior that they use to locate and then attack orb weavers on their webs correlate with web designs (these probably vary immensely: for instance, some bugs utilize tangles beside the orbs of *Argiope* to attack the spiders, while the same tangles probably defend against lizards, wasps, salticids, and damselflies)?

F5. Spider defensive behavior

- Is the high diversity of defensive behavior of *Uloborus glomosus* according to the time of day (Cushing & Opell 1990a,b) typical of other orb weavers? Can the differences be related to the likely danger from different types of predators?

F6. Web designs as defenses against dangerous prey or predators?

- Do species with horizontal orbs suffer less leg loss than those with vertical orbs?
- Do orb weavers suffer more frequent leg loss than linyphiids that have tangles in their webs? Do linyphiid species that lack tangles in their webs suffer more frequent leg loss than those that have tangles (as predicted by arguments of Blackledge et al. 2003a)?

G. Mental processes: attention, learning, sleep, and "understanding"

G1. Attention/concentration, errors, and sleep

- Can some of the variation in construction behavior be attributed to lapses of attention by the spider (test experimentally by attempting to induce "errors": does the consistency of sticky spiral spacing decrease when spiders are subjected to intermittent bright lights, strong sudden sounds, or to gusts of wind? Does the frequency with which *Nephila* skips a radius during temporary spiral construction increase with such distracting stimuli?
- Is there any sign that spider gets tired and loses concentration more when she has to compensate for missing legs (e.g., does sticky spiral spacing get less consistent)?
- Is it more likely (as I suspect) that sudden sounds will induce a spider to interrupt radius construction than during sticky spiral construction (a reduced susceptibility during sticky spiral construction would be compatible, though not proof, of increased attention being needed to weigh the many (>10) variables)?
- In comparions between small vs large webs of the same individual, does the precision of sticky spiral spacing decrease more in the central portion of the larger webs (does the spider get tired from the long concentration building the sticky spiral)?
- Does the alertness of orb weavers (responsiveness to prey impacts) vary differ at different times of the day (predict high when orb is fresh, low when it is tattered)?

- Can spiders learn to ignore disturbing stimuli (as suggested by use of low level sounds and light to reduce interruptions – Eberhard 1990)?
- Are there properties of "attention" in other animals that can be tested for in spiders?
- Do errors in temporary spiral construction by *Nephila clavipes,* such as attaching to the wrong radius, vary with spider age? With site in orb? With distractions? With missing leg II or III? Are there interactions among these factors?

G2. Memory, mental maps and "altered states of consciousness"

- If "double sector" experiments in which 2 loops of temporary spiral are broken in two sectors during sticky spiral construction (e.g. Fig 7.14) are performed in settings in which possible visual, slant and wind cues are eliminated, is the spider still able to distinguish the two modified sites? If not, which of these cues, when added, enables the spider to make the distinction? Does disturbing her concentration with sudden noises, bright lights, or a puff of air increase the frequency with which she is "fooled"?
- What happens when the spider encounters an object (stick/leaf) has been introduced into an empty space that had been previously "explored" during exploration? Is the reaction different when she encounters a similar object introduced into a previously un-explored space (does she have a mental map of what has and has not been explored)?
- Is it possible, in a "double sector" experiment, to confuse the spider regarding the second hole in the temporary spiral by reversing the slant of the web while she is working?
- Do spiders gradually improve how they wrap prey (especially how well they snag wrapping lines with their legs IV) (compare small spiderlings with adults)?
- Does *Zosis geniculata* (UL) remember when it has built only part of web on the first night of a "two night" orb (transfer the spider to complete or other incomplete webs)?
- Is it possible, by observing pauses and the directions of exploratory movements of the legs at sites where the web has been modified experimentally (e.g. break two loops of temporary spiral) to deduce whether spiders have expectations, and what those expectations are (do legs search in certain areas where lines would have been expected to occur)?
- Do *Nephila clavipes* alternate the sides of webs that they repair, and if so (as appears to be the case), is the alternation based on memory of the side repaired the previous day or on stimuli from older portions of the web (could transfer individuals between webs with different sides damaged)?
- Do very young *Nephila* have gigantism traits such as backing up the drag line to return to the hub, or inner loop localization with leg oIV (a negative answer would support adaptive flexibility and insight arguments) (this logic depends on the proportional lengths of legs increasing during ontogeny – measurements would be needed to test this possibility)?
- Do drugs (amphetamine, etc.) interfere with possible cognitive abilities? For instance, does *Leucauge mariana* (TET) have more trouble remembering second sector of TSP removal in "double" expt.? Does *Zosis geniculata* (UL) forget more often about the second and third sectors in two and three sector repair webs? Do drugged spiders respond the same way to Hingston experiments during sticky spiral construction? Are there correlations between spider responses and the effects in humans of different drugs?
- Do 3-lobed repairs in *Z. geniculata* exist in nature (can the ability to selectively ignore certain cues in these situations be attributed to pre-programmed behavioral flexibility; or is it perhaps due to some sort of "understanding" by the spider)?
- Can spiders learn to improve their compensation for leg loss in construction behavior or attack behavior (a larger effect might be expected in attack behavior because of more immediate feedback of rewards)?
- Is it possible, using the logic of reading the mind of a blind man by watching how he moves his cane (e.g., the site probed by a leg can reveal where she expects to find lines) (section 2.4.2.1, 7.1.1), to deduce in detail both the information just acquired previously by the spider (especially in experimentally altered webs) and her expectations (both recent memories and pre-programmed instrutions) (video recordings)? For instance, is the probing behavior when the spider encounters the second hole in the temporary spiral in the "double" experiment different from that when she encountered the first, and does it correlate with whether or not she is "fooled"?

H. Functional morphology, experimental neurobiology

H1. Spinning apparatus, other morphological traits

- Do the surfaces of the spinnerets where spigots occur inflate and deflate during and between attachments to cause the spigots to move? If so, what are the effects of these movements on silk production?
- Are there structures in the ducts of piriform glands that might be associated with the very quick initiation and cessation of piriform silk production?
- How do the anterior lateral spinnerets and the tips where piriform lines are produced move when the spider attaches one line to another? How do these movements compare with those when a line is attached to a flat substrate (Wolff study)?
- Does removal of the trichobothria *Leucauge, Mangora,* or *Uloborus* affect the designs of their webs, their attack behavior, their resting positions at hub, their defensive behavior, or any other behavior?
- How do the spinnerets move during attachments of sticky to non-sticky lines, and of non-sticky to non-sticky lines?

H2. CNS

- Do the tracts in the ganglion of leg IV of *Nephila,* which uses leg to locate the inner loop of sticky spiral and also to climb the dragline to return to the hub, differ from those of other species in which leg IV does not perform these functions?
- Do the tracts in the ganglion of legs IV and III (which is used to substitute for IV to some extent) in *Nephila* change when also when one leg IV is removed? Similarly, do the tracts in the ganglia for legs I nd II change in araneids when one leg I is removed and the ipsilateral leg II takes over the inner loop localization function (legs can be left intact on the other side of the animal and their ganglia can serve as controls)?

- Can the mechanistic details of the behavioral manipulation by larval polysphinctine ichneumonid wasps illuminate the functional anatomy and physiology of nervous control of web construction behavior (timing of gene expression, sites in spider nervous system where larval products accumulate, changes in gene expression in the spider)?
- Are there special sensory structures on the legs that are used in inner loop localization behavior (ventral tip of leg I in araneids, dorsal tip of leg I in tetragnathids, dorsal tarsus-metatarsus of leg IV in *Nephila* and *Micrathena duodecimspinosa*). Does the regularity of sticky spiral spacing decrease when these areas of these legs are covered?

ONLINE Figure Captions

Fig. O6.1 Typical araneid sticky spiral construction behavior by a mature female *Alpaida acuta* (AR) in the outer half of her orb. The spider, seen from her ventral side, was moving downward (the frames are numbered to indicate the seconds elapsed since the previous sticky spiral attachment; sticky lines are thicker than non-sticky lines; the arrow in frame 4.89 indicates the site of contact with the inner loop of the sticky spiral; "tsp" = outer loop of temporary spiral, "inner loop" = inner loop of sticky spiral). The movements which were consistent and important in the extraction and placement of the sticky line and in guiding the spider's attachment behavior are described in Appendix 4A3 (the other legs seemed to mainly support the spider in her web) (from Eberhard 1982).

Fig. O6.2. Typical sticky spiral construction by *Leucauge* sp. (specimen #1556) seen from above as the spider moved counterclockwise on an approximately horizontal orb) (conventions as in Fig. O6.1). Differences with araneids (Fig. O6.1) are described in section O6.3 (from Eberhard 1982).

Fig. O6.3. Typical sticky spiral construction traced from movies of *Nephila clavipes* seen from the ventral side as the spider moved clockwise in the bottom sector of an approximately 60º orb (conventions as in Fig. O6.1). Consistent differences with araneids and tetragnathids are described in Appendix 4A3 (from Eberhard 1982).

Fig. O6.4. These stylized drawings of hub construction behavior by a mature female *M. duodedcimspinosa* were traced from a video recording. *a*) The spider was just about to attach the first loop of hub spiral to radius r_n while she held the center of the hub with leg iIII (arrow); legs oIII and oIV held r_n and pressed it against her spinnerets. Leg iIII did not change the point where it held the hub during construction of the entire first hub loop. The irregularly shaped mass in the center of the hub was the accumulation of loose silk lines that were reeled up and deposited there during radius construction. *b*) As the spider built the second loop (0.3s after attaching to r_{n-1}), she repeatedly contacted the first loop with her palps (arrow). Leg iIII repeatedly shifted positions, and apparently supported the spider's body. Leg oIV still held radius r_{n-1} to which she spider had just attached, while leg oIII had just followed oII to grasp r_n, to which the next attachment would be made; leg oI was about to grasp the next radius (r_{n+1}). Legs iI and iII sometimes also grasped the hub line, but more often they grasped radii inside or outside of this loop; they advanced irregularly, much less frequently than the rate of attachments. *c*) As the spider was just about to attach the fourth hub loop to r_n (some segments of this loop are omitted), legs iI and iII moved "hand-over-hand" (arrow by iI), grasping either the outermost hub loop (leg oII in the drawing), junctions of this loop with radii, or radii nearby (dot shows position of leg oI 0.16s after this drawing); although these legs usually moved in alternation, leg iII did not follow leg iI, and each leg often probed repeatedly before grasping a line; they moved much less frequently than the rate of attachments. Leg oII was about to follow leg oI to grasp point y, and leg oIII was about to follow leg oII to grasp point z. Legs oIV and oIII held r_n against the spinnerets to make the attachment. The distances between points grasped by legs oI and oII, oII and oIII, and by oIII and oIV when they were grasping the same radius were relatively constant; oIII always grasped inside oII (*b*), and oIV grasped outside of oIII (*a*, *c*). After leg oIV grasped the radius being held by oIII, leg probably oIII slid inward along r_n to touch the outer hub loop just before the attachment was made. Legs iIII and iIV moved infrequently and the lines that they grasped varied; they probably functioned simply to support the spider's weight. The palps did not contact web lines during the later stages of hub construction (traced from video recordings; the positions of some radii are only approximate, as some lines were not visible in some frames of the recording).

Fig. O6.5. Diagrammatic steps in secondary radius construction by *Nephila clavipes* (a), *Uloborus diversus* (b) and *Mecynogea lemniscata* (c).

Fig. O6.5a. The arrows in these drawings of repairs of the temporary spiral (above) and sticky spiral (below) by *Cyclosa confusa* (AR) mark "repair" lines that were built across intact portions of the orb. The spider presumably used different cues to guide the attachments in these portions of the repairs than those used in the portions farther from the hub. Note in the lower drawing, for instance, how in the outer portion of the sticky spiral doubled back each time it encountered the edge of the intact web, but failed to double back nearer the hub. In contrast with uloborids (Fig. 6.18) and nephilids (Fig. O6.10), repair did not involve replacement of the hub (from Shinkai 1988a).

Fig. O6.6. The photographs *a* and *b* illustrate frame construction by an *Uloborus diversus* (UL) moving away from the hub on the exit radius (*a*) and attaching the new frame to the new radius just before returning to the hub (*b*). The spider was moving away from the hub on the exit radius during radius construction in *c*, and was in the midst of temporary spiral construction in *d*. The spider (s) appears as a blur in these long exposure photos of uncoated webs.

Fig. O6.7 These diagrammatic sequences illustrate the bewilderingly complex variation in different types of frame construction by *Nephila clavipes* (from Eberhard 1990).

Fig. O6.8 Many radii in the webs of *Nephila* spp. were built as part of temporary spiral construction. The sequence of attachments in *N. clavipes*, illustrated in *a*, shows the double attachments of temporary spiral lines to radii r_{n-2} (at 1 and 2), r_{n-1} (at 3 and 4) and r_n (at 5 and 6), followed by the spider moving to the edge of the web along r_n to attach the first and second new radii. It then returned to the hub to attach the second new radius to the first at 7, and then continued as before, making double temporary spiral attachments to the r_{n+1} (at 8 and 9) and r_{n+2} (at 10 and 11). The inverted "V" patterns marked with arrows in the web of *N. clavipes* in *b* and letters in the web of *N. clavata* in *c* mark sites that correspond to point 7 in *a*, where a pair of new radii originated (the heavy line in *c* marks the edge of a replacement repair sector).

Fig. O6.9 The central areas of finished orbs of the anapid *Anapis keyserlingi* and the mysmenid *Maymena* sp. that were collected on glass slides and observed under a compound microscope illustrate modifications that occurred after the sticky spiral was finished. Each of the *A. keyserlingi* radii marked with a black dot had apparently been broken and then repaired in the free zone, because there was a mass of material (like that indicated by the arrow) near the innermost loop of sticky spiral that was probably piriform silk used to attach lines to each other. The triangles mark three lines that were probably above the plane of the web, because no sticky lines were attached to them in this area of the web. Asterisks mark especially clear double attachments of the hub spiral to radii that presumably tightened the radii. In the drawing of the *M.* sp. web, the thin lines with dots represent sticky lines; elementary radii (thicker lines with a large dot) (all are connected to the hub); and the supplementary radii (thinner lines lacking dots) that end on sticky lines. The 5:00 section of the orb was evidently damaged, probably during collection. The lines extending upward at 11:30 were probably above the plane of the orb. Piriform masses, where elementary radii were probably broken, lengthened, and then repaired are indicated by arrows (from Eberhard 1987).

Fig. O6.10. In this closeup photo of the hub area of a replacement repair of a *Nephila clavipes* orb, the edge of the older portion of the web is marked with arrows. Daily partial replacement of orbs is common in this species. In rebuilding the left half of the hub, and the spider did not replace the rest of the hub, in contrast with the complete hub replacements in similar replacement repairs by the uloborids *Uloborus diversus* and *Zosis geniculata*. A few lines in the tangle alongside the hub are visible (more or less out of focus).

Fig. O9.1. The orb-like tangles that occurred regularly below the horizontal orbs of *Uloborus conus* (UL) (*a*), occasionally beside the vertical orbs of *Allocyclosa bifurcata* orbs (AR) (*b*), and the disorganized tangles near the lower side of the hubs of *Argiope trifasciata* (AR) orbs and resting webs (*c*, *d*) probably represent convergent defenses against predators. In all three species the tangles were always on the side of the web on which the spider rested (occasional exceptions occurred in nearly perfectly vertical *A. bifurcata* webs) (*a* from Lubin et al. 1982 courtesy of Yael Lubin).

Fig. O9.2. This web of a mature male of *Cyrtophora citricola* built in a wire cube, seen in lateral view in *a*, in dorsal view in *b*, and in a closeup dorsal view of the sheet in *c*, offers an argument in favor of phylogenetic constraints. Mature males of this and related species such as *Mecynogea lemniscata* (WE) are unusual in being able to make typical prey capture webs (compare with the mature female webs in Fig. 1.7), perhaps because the webs of this species lack adhesive lines and thus do not require aggregate and pseudoflagelliform gland silk (which are lacking in most mature araneoid males). This association between prey capture webs that lack sticky silk and the construction of prey capture webs by mature males suggests that the loss of sticky silk glands may have constrained the evolution of web construction by mature males of other araneids; this constraint may have condemned them to lives of “crime and abstinence”, robbing webs from immature nymphs, or simply not feeding at all.