Are smaller animals behaviourally limited? Lack of clear constraints in miniature spiders

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Because of scaling trends in physiology and morphology, very small animals are expected to suffer especially strong selection to reduce the cost of the central nervous system, which may make them more likely to sacrifice behavioural capacities to economize on nervous tissue. This 'size-limitation' hypothesis predicts reduced behavioural capabilities in smaller animals. I tested this hypothesis by comparing web construction behaviour of young nymphs and adults of a very small orb-weaving spider, *Anapisona simoni* (young nymphs ~0.005 mg, adults ~0.8 mg), with those of relatives up to 10^4 times larger. In these comparisons I took advantage of the special opportunities offered by orb webs to study fine behavioural details during web construction, because the webs represent precise records of large numbers of behavioural decisions. Combining these results with those of a previous study, the size-limitation hypothesis was not supported: very small spiders failed to show three predicted trends, and they showed four other trends that were in directions opposite to those predicted by the hypothesis. Two additional intraweb comparisons (at least one of which was probably biased against equal performance by the smallest species) gave a mix of support and lack of support for the predictions, while only one interspecific difference supported the predictions. Other studies have shown that small spiders have relatively large central nervous systems for their body sizes, suggesting that they may maintain behavioural capabilities comparable to those of larger orb weavers by paying the material and metabolic costs of building and maintaining large volumes of nervous tissue. These considerations may have general consequences for the probability of evolving small body sizes and egg sizes in spiders and other animals.

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The question of whether smaller animals tend to have reduced mental powers has a long history. Rensch (1960, page 165) concluded, from comparing the abilities of races of domestic fowl, mice, rats, fish and elephants to learn and to retain lessons, that '... the races or species of larger body size show better capabilities of learning, memorizing, and perhaps also transposing (abstracting) than smaller related races or species'. The detailed, quantitative behavioural observations needed to document this idea are sparse, however, and some later authors such as Bonner (2006, page 55) have not found Rensch's conclusion convincing ('I cannot believe that Rensch's intriguing idea has been an important factor in evolution. There are too many small animals of remarkable intelligence, such as parrots and crows among others').

At body sizes substantially below those of the vertebrates discussed by Rensch (1960) and Bonner (2006), there are additional reasons to suppose that very small body size may impose

behavioural limitations. This is because in very small animals the balance between the costs of building and maintaining the central nervous system (CNS), as opposed to the benefits of the resulting behavioural capabilities that it provides, is expected to tilt more strongly towards costs. This expectation is based on several considerations. There is a general trend for smaller animals to have larger central nervous systems relative to their body sizes (Beutel et al. 2005; Bonner 2006; Wehner et al. 2007; Polilov & Beutel 2009; Seid et al., in press); the causes of this trend are not certain (Striedter 2005). Nervous tissue is relatively more costly to maintain than are other types of tissue (e.g. Attwell & Laughlin 2001; Niven et al. 2007), so a larger CNS imposes disproportionate metabolic costs. In addition, smaller animals tend to have smaller neurons, and metabolic costs may be relatively higher in smaller neurons. The surface area of a neuron is positively related to its energy consumption (Niven et al. 2007), and smaller neurons have proportionally larger surface areas, so comparable information-processing capabilities in a smaller brain will result in increased costs due to higher density of metabolic activity (Niven et al. 2007; Chittka & Niven 2009). Furthermore, there may also be lower limits on the sizes of functional axons, due to spontaneous opening of

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voltage-gated ion channels (Faisal et al. 2005). Additionally, there may be a lower limit to neuron size imposed by the nucleus, as the percentage of the cell occupied by the nucleus is larger in smaller cells (Polilov & Beutel 2009). Reduction in neuron and axon size to maintain similar connectivity in miniaturized animals will be limited if their neurons reach these critical sizes.

These considerations lead to the expectation that there may be especially strong selection to reduce the costs of brains in very small animals. Strong selection to economize on the costs of their CNS could make very small animals less likely to evolve new behavioural capacities, or to maintain capacities they have inherited from larger ancestors. This suggests the 'size-limitation' hypothesis for behaviour: very small animals will tend to exhibit reduced behavioural capacities and adopt lifestyles that require less behavioural capability. An alternative to this hypothesis is that the benefit from maintaining behavioural capacities is great enough that very small animals maintain behavioural capacities and pay disproportionately high material and energetic costs to have relatively large brains (the 'oversized brain' hypothesis). In this case they would be expected to possess behavioural capabilities that are comparable to those of larger species. A third possibility is that smaller species achieve greater nervous system efficiency (the 'neural tricks' hypothesis). Several possible mechanisms could be employed. Behavioural capacities could be maintained while sacrificing flexibility in their expression, as in the 'matched filters' of Wehner (1987). Intrinsic, adaptive biases in sense organs could in effect perform peripheral pre-analyses of stimuli that would otherwise have to be performed centrally (Fratzl & Barth 2009). The mechanical properties of effector organs could provide partial guidance for otherwise ballistic movements (Seid et al. 2008; Chittka & Niven 2009). Greater efficiency could also come from nonspiking interneurons or multifunctional neurons (Chittka & Niven 2009). The neural tricks hypothesis predicts maintenance of similar behavioural tasks, but perhaps less flexibility in performing them.

These three hypotheses, which are not new (Chittka & Niven 2009), are not mutually exclusive. Their relative importance in very small animals is as yet unclear. The question asked here is empirical rather than theoretical: do very small animals tend to have reduced behavioural capacities compared with those of larger animals, perhaps associated with allometric constraints on the relative sizes of their nervous systems?

Evaluating these hypotheses requires both morphological and behavioural data. Morphological studies show that the brains of very small species of insects and spiders are smaller in absolute terms than those of larger species, as in vertebrates (e.g. Rensch 1960; Bonner 2006), however, they are proportionally much larger (Beutel et al. 2005; Wehner et al. 2007; Polilov & Beutel 2009; Seid et al., in press). For example, in first-instar larva of the ptiliid beetle *Mikado* sp. and in adult workers of *Pheidole* ants, both of which are extremely small insect species (∼0.04 mg), the brain is 15–16% of the total body volume or mass (compared to about 2.5% in humans; Polilov & Beutel 2009; Seid et al., in press, unpublished data); this percentage is about 750 times larger than that for the brain of a large water beetle (Beutel et al. 2005). In the tiny beetles and in the small first-instar larva of a strepsipteran, the brain extends out of the head capsule and into the prothorax (Beutel et al. 2005). The brains of very small orb-weaving spiders are also relatively large, and portions extend into the coxae of the legs and palps (R. Quesada, E. Triana, G. Vargas, M. Seid, J. Douglass, J. Niven, W. Eberhard & W. Wcislo, unpublished data).

Are the proportionally larger brains of these tiny animals sufficiently large to allow them to maintain behavioural abilities comparable to those of their larger relatives? Or has selection to reduce the cost of the brain (which is likely to be particularly strong with such relatively large brains) resulted in reduced behavioural

capacities? The behavioural data needed to answer such a question are very scarce. Beutel et al. (2005) and Polilov & Beutel (2009) speculated that there may be no behavioural impairment in the tiny larvae whose morphology they studied, but their arguments cited only the fact that the larvae have sense organs and are able to move about. There are apparently no direct behavioural observations of insects in this size range that might reveal possible manifestations of reduced behavioural abilities, such as increased error rates, slower execution, decreased behavioural repertoires, or other relevant variables. Several studies of insects attempted to assess predicted reductions in behavioural complexity as a consequence of miniaturization (Howse 1974; Eisenberg & Wilson 1978; Harvey et al. 1980; Eisenberg 1981; Cole 1985), but yielded unconvincing and contradictory results. As pointed out by Cole (1985), some studies (Howse 1974; Eisenberg & Wilson 1978; Harvey et al. 1980; Eisenberg 1981) were unconvincing because of the lack of objective criteria for measuring 'complexity'. Cole (1985) attempted to quantify complexity objectively by comparing repertoires, and demonstrated a positive correlation between head size and the number of behavioural tasks performed by a given species of ant. These data are also problematic, however, for several reasons. There were no clear criteria for distinguishing behavioural tasks; different tasks are not necessarily equally demanding with respect to neural capabilities, so simple counts may be misleading. The rate of errors in a given task and the speed and agility with which it is performed were not measured. And head size does not necessarily show the same relation to brain size in different species (the brains of smaller species may be larger compared with their head sizes; Beutel et al. 2005; Polilov & Beutel 2009; J. Douglass, unpublished data). Controls for phylogenetic inertia (Harvey & Pagel 1991) were also lacking. Furthermore, studies of the same sort with other social insects (which suffered from most of the same problems) yielded contradictory results: either a lack of correlations (minor *Pheidole* ant workers: Wilson 1984), or correlations in the opposite direction (termites: Howse 1974; major *Pheidole* ant workers: Wilson 1984).

The results of one previous quantitative behavioural study, comparing very small orb-weaving spiders (weighing <0.005 mg) with other orb weavers (weighing up to about 60 mg) contradicted the size-limitation hypothesis. The precision in spacing loops of sticky spiral lines from each other during orb construction was similar (or somewhat better) in the very small spiders compared with that of their larger relatives (Eberhard 2007). This behavioural task may be relatively undemanding, however, compared with some other tasks in orb construction (Eberhard 2007). Thus, these results do not eliminate the possibility that very small spiders do have behavioural deficits, but that they are only manifested in the execution of more demanding behavioural tasks. The object of the present study was to search for differences in additional, probably more demanding behaviour patterns associated with orb web construction in this same set of spiders. I examined both behavioural flexibility (the ability to adjust behaviour to different circumstances) and the precision of these adjustments.

METHODS

Orb weavers are particularly suited to fine-grained behavioural comparisons because their webs constitute detailed, unusually precise records of behavioural decisions (Zschokke & Vollrath 1995). In addition, because the stimuli guiding the spider during construction are largely derived from the distances the spider travels and the lines it contacts (Hingston 1923; Eberhard 1969; 1972, 1987a; Vollrath 1992; Krink & Vollrath 1999; W. G. Eberhard & T. Hesselberg, unpublished data), both possible stimuli and behavioural responses to them can be measured with unusual precision, especially for tiny animals. Orb construction behaviour is

highly ordered, starting with exploration of the area in which the web will be built, followed by frame and early ('primary') radius construction, then construction of further radii built after primary frame construction ('secondary radii'), fastening the radii together with hub lines, then construction of a scaffolding (temporary spiral) working outward from the hub, and finally construction of the sticky spiral (working from the edge inward) (Hingston 1923; Eberhard 1982; Vollrath 1992). Most orbs are planar, but in a few species (including *Anapisona simoni* of this study) the orb forms a cone (Fig. 1). These traits of orbs permitted a variety of analyses, including documentation of an alternative web design, and the ability to make flexible adjustments of several aspects of typical orb design on the basis of other variables (adjustment of the degree of inclination of the plane of the orb based on an estimation of the horizontal area available in which to build; adjustment of spaces between sticky spiral loops based on preceding spaces on the same radius; adjustment of the number of sticky spiral loops based on the number of radii; adjustment of the angles between radii based on the lengths of the radii; and adjustment of the number of sticky lines above the orb based on the number of radial lines above the orb). The abilities of very small and larger spiders to make these adjustments could thus be compared.

Table 1
Sizes of spiders in this study

		Length (mm)	Mass (mg)
Anapidae			
Anapisona simoni	Nymph[*]	0.6	<0.005
	Adult	1.0–1.3	0.6–1.0
Araneidae			
Allocyclosa bifurca	Nymph[†]	1	0.8
	Adult female	6	30
Micrathena duodecimspinosa	Adult female	8	45
Tetragnathidae			
Leucauge mariana	Adult female	7	40–80

[*] Smallest size class found in the field.
[†] First instar outside the eggsac.

Different-sized individuals of three species of orb-weaving spiders were studied near San Antonio de Escazu, Costa Rica (elevation 1325 m; 9°56′N, 84°5′W) along with a fourth near Gamboa, Panama (elevation ca. 30 m; 9°7′N, 79°42′W) (Table 1). The smallest species, *A. simoni*, belongs to a family (Anapidae) of very small spiders thought to have evolved from larger ancestors (Griswold et al. 1998; Lopardo et al., in press). In all species, only a single web from each individual spider was measured. Except for
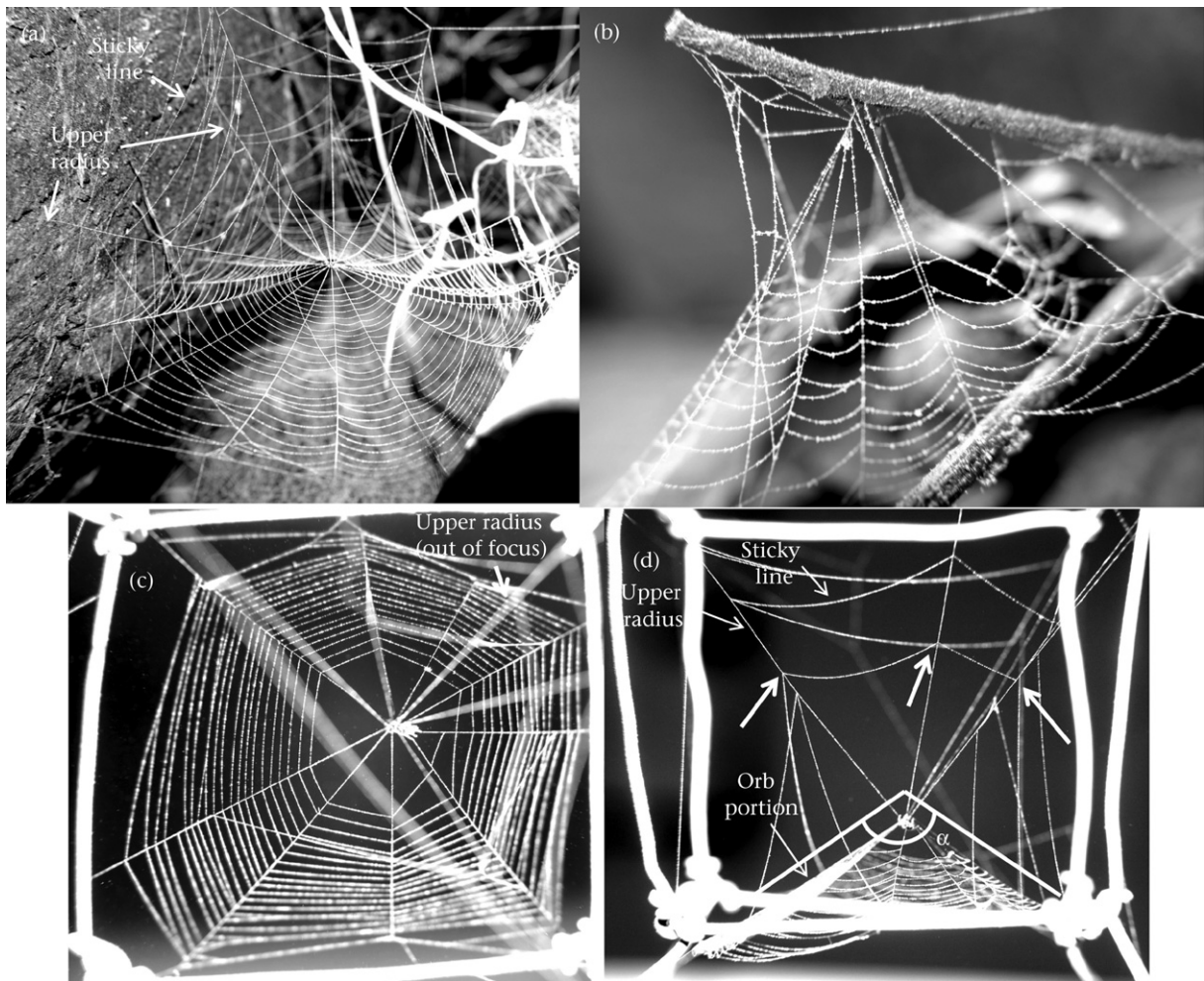

Figure 1. Webs of adult female *A. simoni* in the field (a, b) and in the laboratory (c, d), showing 'typical' orb forms (a, c, d) and the alternate 'orb sector' web design (b) in which the spider rested under the twig (panels (c) and (d) show dorsal and lateral views of the same web). The unlabelled, heavy arrows in (d) show attachment points of sticky line above the orb that was attached to several upper radii at similar distances from the hub but far from the previous loop; because spiders never go beyond the attachment site along the radius during sticky spiral construction (Eberhard 1987b), such regular spacing implies the ability to sense (and standardize) the distance moved along the radius. More nearly planar orbs had larger angles at the hub (α in (d)).

adult *Allocyclosa bifurca*, all webs in captivity were the first webs that each spider built, almost always after no more than 1 day in captivity. Weights were measured on electric balances.

I used both intraspecific comparisons, which controlled for possible differences between species (thus making corrections for phylogenetic inertia unnecessary), and interspecific comparisons, which did not control for species differences, but permitted greater ranges in size.

Digital photographs of *A. simoni* webs that had been coated with talcum powder (Fig. 1c, d) were made in the field, and in captivity (usually on the same or the following day). Captive spiders were placed in wire cubes (Fig. 1d) that were placed in small containers with water in the bottom to encourage spiders to attach all their lines to the cube. Webs in cubes were coated with talcum powder and photographed in dorsal and lateral views from each of two adjacent sides (Fig. 1c, d). The length of each radius was calculated from its length seen in dorsal view corrected for its angle with horizontal; the length in the photograph in dorsal view was divided by the cosine of the angle of the radius with horizontal, as estimated from photographs of lateral views of the web. I determined the maximum number of sticky lines attached to any given radius above the plane of the orb ('upper radius' in Fig. 1) by direct observation of webs both in captivity and in the field, as this detail was not clear in photographs.

To quantify behavioural flexibility in response to the amount of available space in which to build a web, I offered mature *A. simoni* spiders two sizes of cubes, large (5.0–5.5 cm on a side) and small (3.4–3.8 cm on a side). The angle at the hub of the cone formed by the orb, an apparent response variable, was estimated as the mean of the cone angles (α in Fig. 1d) in the two lateral views of the web. Angles were measured using the program ImageJ (National Institutes of Health, Bethesda, MD, U.S.A.).

I photographed webs built by *Leucauge mariana* and *A. bifurca* on wire hoops in captivity after coating the webs with corn starch. Reflecting the orientations of their orbs in nature, the 50 cm diameter wire hoops for *L. mariana* (Eberhard 1987a) were hung horizontally, while those for *A. bifurca* (about 20 cm diameter) were vertical; webs were photographed perpendicular to the plane of the orb. Webs of *Micrathena duodecimspinosa* were photographed in the field after being coated with corn starch; photographs were perpendicular to the plane of the orb (the mean angle with horizontal was $74.5 \pm 7.3°$ in 70 webs).

Orb-weaving spiders generally adjust their orbs according to the spaces and attachment sites that are available, and to other aspects of the web itself (Ades 1986; Vollrath 1992). I tested the abilities of spiders of different sizes to make such adjustments by testing for significant correlations between web traits and other variables in two-variable regression analyses, in which the portion of the web that was built first was the independent variable. For instance, in the analysis of radii and sticky spiral loops, the number of radii was the independent variable and the number of sticky spiral loops was the response variable, because radii are constructed before the sticky spiral. If there was a significant relation, I further evaluated the prediction of the size-limitation hypothesis that smaller animals would make less precise adjustments, and thus show greater scatter around regression lines. For each point, I determined the residual and divided this value by the value predicted by the regression. I compared this measure of the amount of scatter in different species or size groups using a one-way ANOVA with a Hartley test.

I examined whether spiders made 'compensatory' reductions in sticky spiral spacing after having made an oversized space on the same radius by locating oversized spaces (>150% of the mean of spaces immediately preceding and following on the same radius) and then measuring them and the sticky spiral spaces nearby (Fig. 2) with ImageJ. I excluded sites with several oversized spaces in a row (e.g. arrow in Fig. 2, left panel) to standardize the measurements and the probable stimuli experienced by the spiders (because memory of changes in distance travelled inward and outward to make attachments immediately preceding a given

Figure 2. On the left, compensatory adjustments of sticky spiral spacing following oversized spaces (white rectangles) in a *M. duodecimspinosa* orb. The oversized space marked with an arrow on the left is shown at greater magnification on the right (labelled 'b'), with the subsequent, compensatory adjustment ('c') and other nearby spaces ('a', 'd', 'e', 'f', 'g'), along with the calculations used to test for compensatory spacing.

attachment is important; W. G. Eberhard & T. Hesselberg, unpublished data). Two comparisons of the possible 'compensatory' space ('c' in Fig. 2, right panel) were made: with the mean spacing at adjacent attachments of the same loop ('c' versus '(d + e)/2' in Fig. 2, right panel); and with the mean of five nearby spaces ('c' versus '(a + d + e + f + g)/5' in Fig. 2, right panel). Means ± SD are reported.

RESULTS

Behavioural Flexibility: Adjustments of Web Variables to Each Other

Radius lengths versus angles

It has long been known that longer radii in orbs tend to make smaller angles with adjacent radii than do shorter radii (Hingston 1923; Koenig 1951; Mayer 1952; LeGuelte 1966; Eberhard 1972). This relationship is thought to result from behavioural adjustments during radius construction that adaptively preserve minimum spaces between radii in the outer portions of orbs (Hingston 1923; Peters 1937; Eberhard 1972). When data were combined from different webs, there was a significant negative relation between radius length and radius angles in all species and sizes (Fig. 3, Table 2).

Because the behaviour thought to be responsible for producing this correlation occurs during the production of secondary radii but not during that of primary radii (LeGuelte 1966; Vollrath 1992; Zschokke 1996), and because the webs of different species in this study have different mixes of primary and secondary radii (see Discussion), I tested the effects of spider size with intraspecific rather than interspecific comparisons. Contrary to predictions of the size-limitation hypothesis, comparisons in both A. bifurca and A. simoni showed similar amounts of scatter around regression lines

Table 2
Strength of the relation between radius length and inter-radius angle

	Slope	F	df	P	Mean absolute residual/predicted	P
Anapisona simoni						
Tiny nymphs (283, 30)*	−0.16	7.67	1, 281	0.006	0.247±0.202	NS[†]
(log-transformed data)	−0.17	8.09	1, 281	0.005	0.247±0.203	
Adults (335, 30)	−0.35	47.6	1, 333	0.000	0.252±0.198	
(log-transformed data)	−0.37	51.7	1, 333	0.000	0.249±0.195	
Allocyslosa bifurca						
Tiny nymphs (847, 36)	−0.25	54.9	1, 845	0.000	0.311±0.298	NS[†]
(log-transformed data)	−0.39	151.8	1, 845	0.000	0.169±0.139	
Adults (731, 20)	−0.30	69.8	1, 728	0.000	0.306±0.278	
(log-transformed data)	−0.30	71.1	1, 728	0.000	0.306±0.280	
M. duodecimspinosa						
Adults (1771, 38)	−0.47	165	1, 1768	0.000	0.222±0.241	
(log-transformed data)	−0.18	59.4	1, 1768	0.000	0.222±0.240	

* Values in parentheses are the number of measurements and the number of webs, respectively.
[†] Comparisons between species were not performed (see Discussion); neither untransformed nor transformed data showed significant differences.

for nymphs and adults (Table 2). Not all data were normally distributed (Fig. 3), so similar tests were made using log-transformed data; they gave similar results (Table 2).

Number of radii versus maximum number of sticky spiral loops

In orb weavers in general, there is a significant positive correlation between the number of radii in a web and the number of loops of sticky spiral in both intra- and interspecific comparisons (Tilquin 1942; Emerit 1968; Eberhard 1972, 1986). All species and sizes of spiders in this study showed significant positive correlations between the number of radii and the maximum number of sticky spiral loops (Fig. 4, Table 3). The scatter around the regression
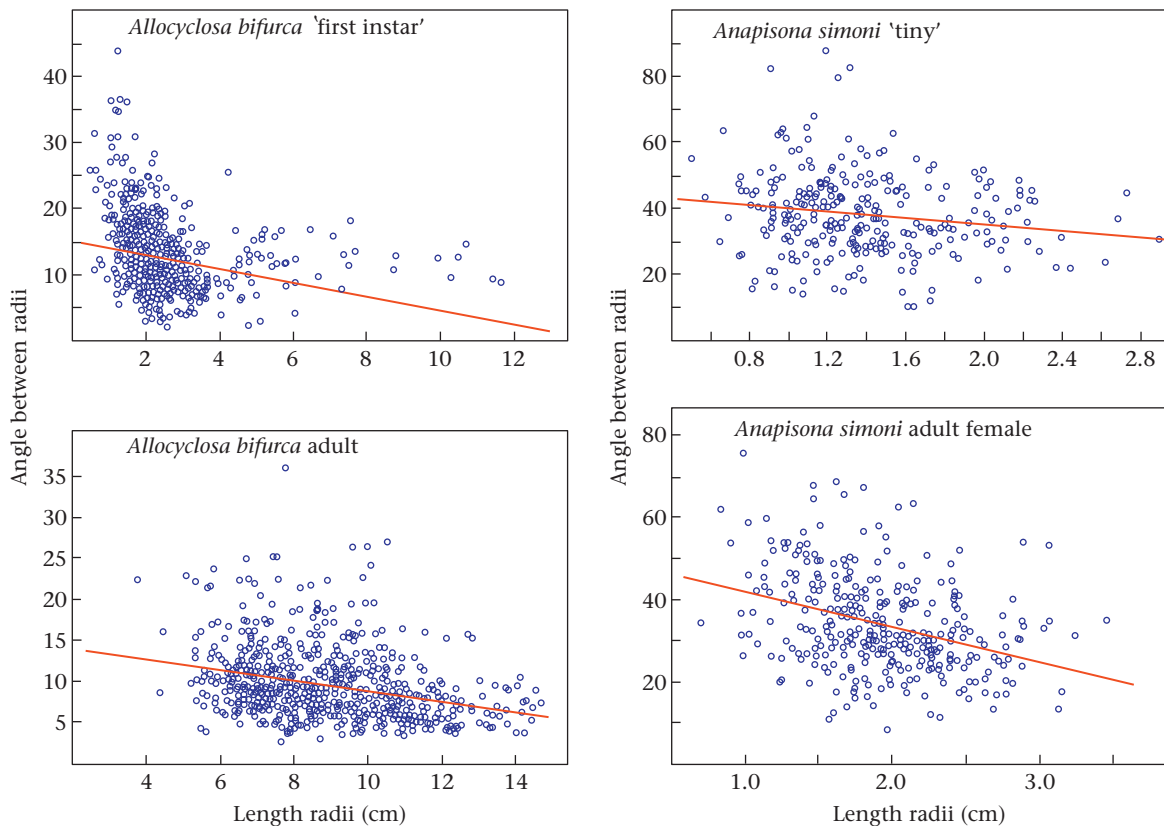

Figure 3. Relations between the mean length of two adjacent radii and the angle between them in different species and sizes.

line was significantly greater in *A. simoni* than in the larger species, and significantly greater in small nymphs than in adult *A. bifurca* (Table 3), fitting predictions of the size-limitation hypothesis. The intraspecific comparison in *A. simoni* did not follow predictions, however, as the scatter was not greater in small nymphs than in the adults.

Adjustments by A. simoni *in the third dimension*

The webs of *A. simoni* nearly always had one or more upper radii (Fig. 1). There was a positive correlation, both in the webs of adults and in those of small nymphs, between the number of upper radii and the maximum number of sticky lines attached to any single upper radius (Fig. 5). The correlation was not stronger in webs of adults than in webs of early nymphs (Table 4). The scatter of points around the regression line was not greater in the webs of small nymphs than in webs of adults (Table 4). None of the other larger species built radial or sticky lines out of the plane of the orb.

Compensatory spaces between loops of sticky spiral following oversized spaces

Still another possibly general trend in orb weavers is a reduction in the sticky spiral spacing immediately following an attachment at an unusually large space ('c' in Fig. 2, right panel). Such adjustments

Table 3
Strength of the relation between the number of radii and the maximum number of sticky spiral loops

	R	F	df	P	Mean absolute residual/predicted
Anapisona simoni					
Adults (115)[*]	0.69	92	1, 113	0.000	$0.20+0.14c_2$
Early instars (52)	0.36	7.63	1, 50	0.008	$0.19+0.15c_1b_1$
Allocyclosa bifurca					
Adult females (28)	0.88	103	1, 30	0.000	$0.10+0.09b_1$
Small nymphs (39)	0.84	86.5	1, 37	0.000	$0.17+0.14$
Leucauge mariana (139)	0.75	182	1, 137	0.000	$0.12+0.10c_{1,2}$
Micrathena sexspinosa (228)	0.73	264	1, 226	0.000	$0.14+0.12$
M. duodecimspinosa (60)	0.79	99.4	1, 58	0.000	

[*] Values in parentheses are the number of measurements.

reduce irregularities in the path of the inner loop of sticky spiral during sticky spiral construction, and are probably triggered by differences in the distances travelled inward and outward on consecutive radii as the spider builds the sticky spiral (Krink & Vollrath 1999; W. G. Eberhard & T. Hesselberg, unpublished data). As predicted by the size-limitation hypothesis, compensatory adjustments were more common in orbs of larger spiders. They
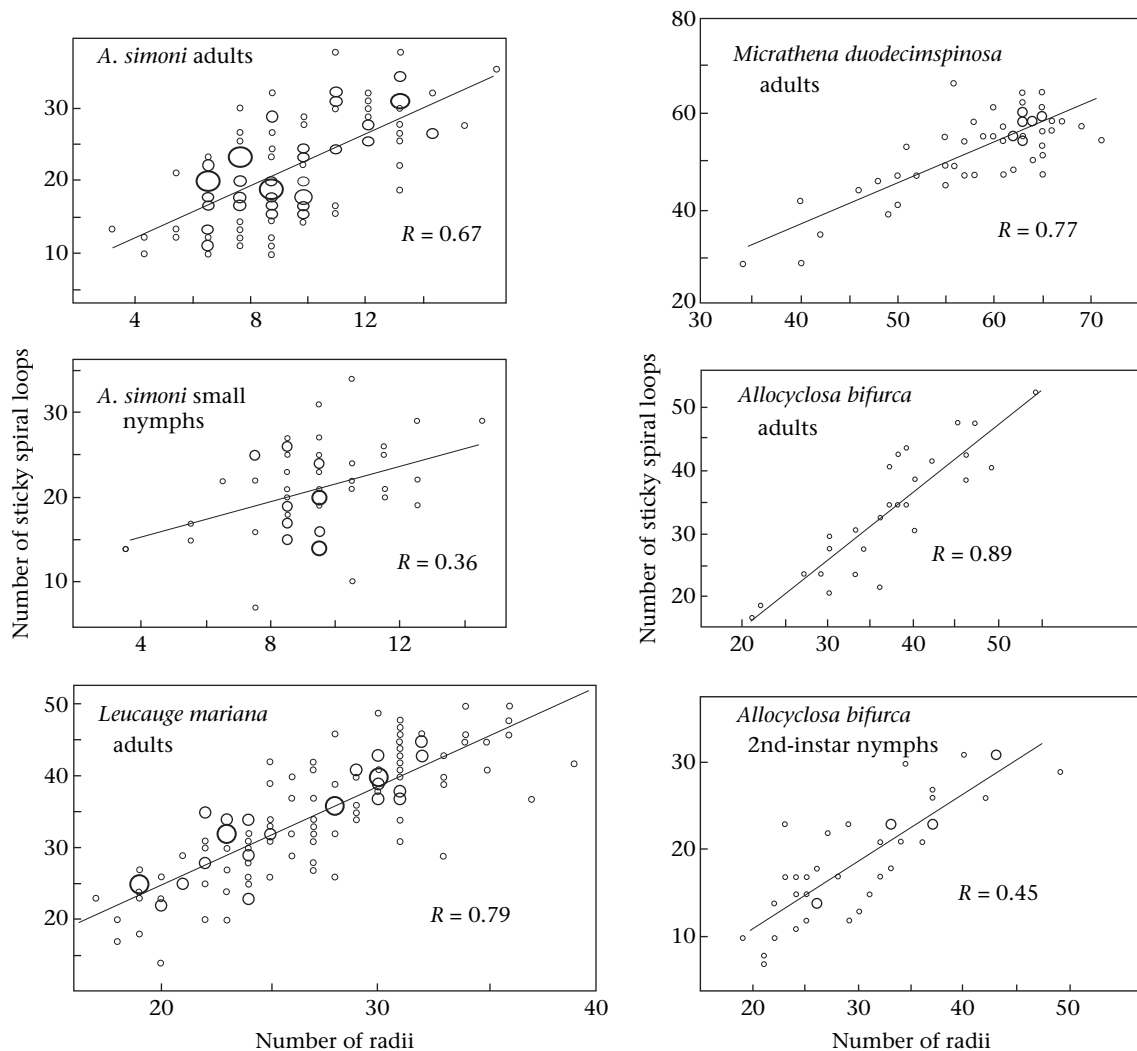

Figure 4. Relation between the number of radii and the maximum number of sticky spiral loops in orb webs of different species and sizes of spiders.
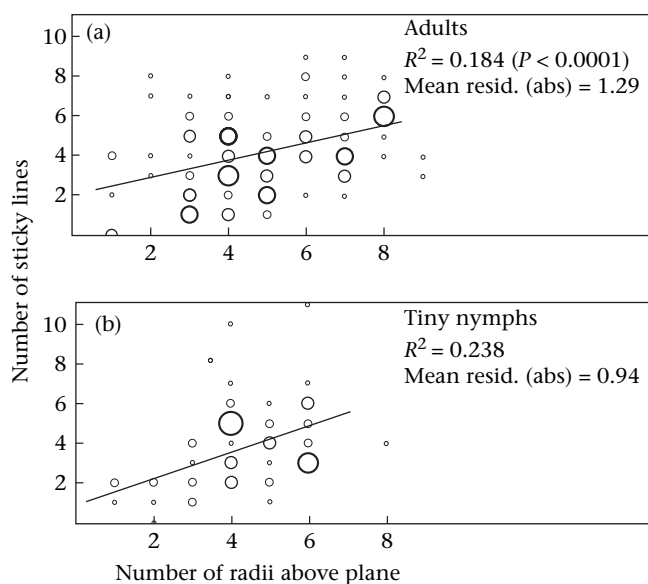
Figure 5. Relation between the number of upper radii and the maximum number of sticky lines attached to an upper radius in field and laboratory webs of adults (above) and small nymphs (below) of *Anapisona simoni*.

occurred in the webs of *M. duodecimspinosa*, *L. mariana* and *A. bifurca*. In the webs of the smallest species, *A. simoni*, they were either lacking (adults), or showed a trend in the opposite direction (nymphs) (Table 5). One size-limitation prediction was not fulfilled, however, as compensatory adjustments were not significantly less frequent in webs of nymphs than in webs of adult *A. bifurca*.

Behavioural Flexibility: 'New' Abilities to Adjust Web Design to External Conditions and Make Alternative Webs

I argued above that some previous studies are difficult to interpret because they failed to convincingly quantify the difficult concept of 'complexity' of behaviour (for a cogent discussion of problems with 'complexity' in spider webs, see Vollrath 1992). There is a way, however, in which it may be possible to obtain a preliminary, qualitative indication of 'complexity' (for possible limitations, see Discussion): if species A and B execute all the same behavioural patterns with the same apparent precision, and species B in addition performs behaviour patterns not performed by species A, then it seems reasonable to conclude that the behaviour of species B is more complex than that of A. Comparisons of repertoires revealed two additional important behavioural contrasts between large and small species.

Adjustments of the orbs of A. simoni to available space

Orb portions of adult *A. simoni* webs were drawn upward more sharply when webs were built in smaller rather than larger wire cubes (mean cone angles for webs in small and large cubes were

Table 4
Strength of the relation between the number of upper radii and the maximum number of sticky lines attached to an upper radius in adults and early instars of *Anapisona simoni*

	R	F	df	P	Mean absolute residual/predicted	P
Adults (106)[*]	0.429	23.5	1, 104	0.000	0.327±0.242	NS
Early instars (57)	0.488	17.2	1, 55	0.0001	0.283±0.221	

Statistical significance was tested using chi-square tests.
  [*] Values in parentheses are the number of measurements.

Table 5
Strength of the relation between the frequency of compensatory adjustments ('c') following oversized spaces between loops of sticky spiral

	c<other nearby spaces (a, d, e, f, g)[*]		P
	c<(d+e)/2	c<(a+d+e+f+g)/5	
Micrathena duodecimspinosa (96, 11)[†]	75.3%	85.9%	0.000, 0.000
Leucauge mariana (90, 11)	62.5%	64.8%	0.001, 0.000
Allocyclosa bifurca			
Adult females (164, 8)	78.0%	69.0%	0.000, 0.0003
2nd-instar nymphs (206, 17)	68.0%	65.3%	0.000, 0.000
Anapisona simoni			
Adults (121, 24)	40.5%	36.5%	0.04, 0.06
Early instars (71, 15)	42.3%	30.8%	0.3, 0.005 (larger)[‡]

Statistical significance was tested using chi-square tests.
  [*] Letters correspond to details of web construction in Fig. 2.
  [†] Values in parentheses are the number of measurements and the number of webs, respectively.
  [‡] The difference was in the opposite direction to that predicted by the size-limitation hypothesis.

$115 \pm 22°$ and $127 \pm 16°$, respectively; Fig. 1d; Mann–Whitney U test: $Z = -2.31$, $N_1 = N_2 = 30$, $P = 0.021$). No such adjustments occurred in webs of the other species, which built only planar or nearly planar orbs. The plesiomorphic state for orb weavers is planar orbs with no additional lines (Griswold et al. 1998), so this ability in anapids is derived.

Alternate web forms in A. simoni

Five of approximately 150–200 webs of adult *A. simoni* seen in the field differed substantially from the typical orbs of this species. Their designs were all very similar and no intermediate web forms were seen, suggesting that the alternate designs were not simply 'mistakes'. They consisted of only of a single more or less planar sector of an orb and lacked a discrete hub. The radii did not converge at a single point, but only in a general area near the underside of a twig or other large object under which the spider rested; some radii were even attached directly to the substrate (Fig. 1b). Three spiders captured on such an 'orb sector' web in the field built a normal complete orb (Fig. 1c, d) when placed on a wire cube in captivity. None of approximately 30 small nymphs found in the field had orb sector webs, but small nymphs and alternate webs were both infrequent, so it is not certain whether nymphs build this type of web. Alternative web forms were never seen in samples of hundreds of orbs of *L. mariana*, *A. bifurca*, *M. duodecimspinosa* and *Micrathena sexspinosa* in the field.

DISCUSSION

Evidence against the Size-limitation Hypothesis

In general, the results of this study, as well as those of previous studies of behavioural precision (Eberhard 2007; Hesselberg 2010), contradict the size-limitation hypothesis that smaller animals are more limited in their behavioural capabilities. In the present study, there were four trends that were opposite those predicted by the hypothesis, three cases in which the predicted trends did not occur, and only three partial confirmations (Table 6). Because intraspecific as well as interspecific comparisons were involved, and most spiders in this study were distantly related phylogenetically, phylogenetic inertia was probably not a problem in these analyses.

Simply summing up the numbers of contradictions and confirmations is probably not appropriate, however. This is because the behavioural capabilities involved are truly apples and oranges, and

Table 6
Summary of the tests of predictions of the size-limitation hypothesis in this and a previous study (Eberhard 2007)

Predictions for smaller individuals	Findings	Test of prediction
Diminished ability to adjust design	Weaker correlation between number of sticky spiral loops and number of radii (but no difference between nymphs and adults of *A. simoni*)	Confirmed
	Failure to adjust sticky spiral space to a previously oversized space in nymphs	
	and adults of *A simoni* (but this task may be especially difficult in this species)	
Diminished complexity of orb design	Lack of temporary spiral in orbs of smallest species	Confirmed
Less 'complexity' than in larger spiders	Alternative orb design present in smallest species	Contradicted (observed trend was opposite to that predicted)
	Adjustment of number of sticky lines to number of radii above the orb only in smallest species	
	Adjustment of cone angle to area available for the orb only in smallest species	
Stronger correlation between radius length and radius angle in larger individuals	Similar strength of correlation between radius length and radius angle in large and small conspecifics	Contradicted (observed trend was opposite to that predicted)
Diminished ability to adjust radial angles to radius length	Nymphs did not differ from adults in *A. simoni*, *A. bifurca*	Contradicted (failure to find the predicted trend)
Weaker correlation between number of upper radii and sticky lines attached to them	Strength of correlation was similar in nymphs and adults	Contradicted (failure to find the predicted trend)
Greater imprecision in spacing of sticky spiral	No trend with body size between or within species (Eberhard 2007)	Contradicted (failure to find the predicted trend)

there is reason to believe that some comparisons are more important or convincing than others. These additional considerations favour rejection of the size-limitation hypothesis.

One weak confirmation of the hypothesis

Using the strength of correlations between variables, as indicated by the scatter around the regression line, to estimate behavioural precision is based on the supposition that deviation from the correlation is the result of imprecision on the part of the spider. This reasoning is only compelling if the independent variable truly causes the changes in the response variable, and if it is the only variable responsible for such changes. If, for example, in one species of spider a second independent variable is included in determining the values of the response variable, this influence could manifest itself as an increase in the 'noise' in the correlation with the first independent variable. In this case, some within-web correlations might be less trustworthy than others. This uncertainty applies to the correlation between the numbers of radii and sticky loops (which generally supported the size-limitation hypothesis). A second weakness of this particular confirmation of the size-limitation hypothesis was that it was only partial: there was no difference in intraspecific comparisons of nymphs versus adults of *A. simoni*.

Alternative explanations for two confirmations
The Weber–Fechner law. I argued above that one apparent confirmation of the size-limitation hypothesis, concerning compensatory spacing of the sticky spiral, is perhaps of limited importance. The reason for this merits further discussion. The smallest species, *A. simoni*, failed to make compensatory adjustments in sticky spiral spacing as seen in the other larger species (Table 5). This lack of compensatory adjustments may well be an indirect consequence of the loss of temporary spiral lines in the webs of this family, rather than a lack of behavioural capabilities. As shown in Fig. 6, anapids travel much larger distances (in relation to their body size) from one attachment of sticky spiral to the next during sticky spiral construction than do most other orb weavers. The Weber–Fechner law states that there is a negative correlation between an animal's ability to detect just noticeable differences for a given stimulus and its perceived intensity (Shettleworth 2010). An extension of this idea would be that when animals measure larger distances, their absolute precision is reduced. For a human, for instance, it is more difficult to measure a longer distance (e.g. 100 m) to the nearest mm than it is to measure a short distance (e.g. 1 cm). For this reason, *A. simoni* is less likely to be able to sense small differences between the relatively long distances it travels inward and outward during sticky spiral construction.

These distances were postulated to influence sticky spiral spacing in *Araneus diadematus* (Krink & Vollrath 1999), and have been demonstrated to do so in *L. mariana* and *M. duodecimspinosa* (W. G Eberhard & T. Hesselberg, unpublished data). Apparent measurement of these distances has also been documented during temporary spiral construction by *L. mariana* (Eberhard 1987a). Thus these distances, which the smallest spiders are likely to measure less precisely, are likely to influence sticky spiral spacing in anapids also. Other more direct evidence also suggests that *A. simoni* probably utilizes the distance travelled inward and outward in deciding where to attach sticky spiral lines to upper radii: attachments of sticky lines to upper radii were often at approximately the same distance from the hub as attachments immediately preceding
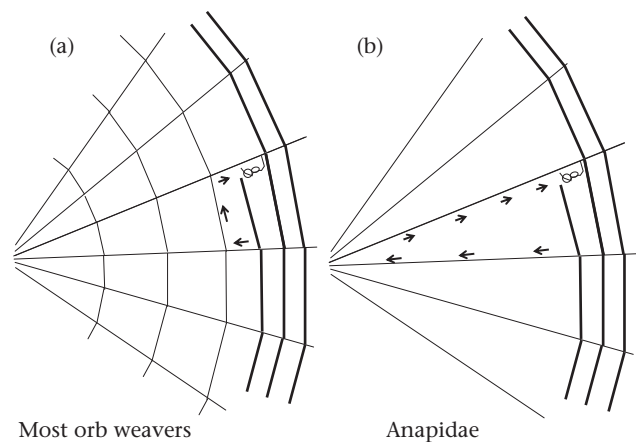

Figure 6. Relative distance (in terms of the spider's body) that a spider travels inward and outward during sticky spiral construction when (a) there is a temporary spiral in its orb and (b) the web lacks a temporary spiral. Scale of the drawings of the spider is approximate.

them in the orb itself. This occurred even when only a single line was attached to this radial line, and there was thus no information available to the spider from previous lines attached to this radial line. In cases in which successive attachments of sticky line were to upper radii, they were often evenly spaced from previous lines, even though the sticky lines were too far apart for the spider to be able to have touched the first line while placing the second (Fig. 1). Similar patterns occur in the webs of other symphytognathoid species and the related family Theridiosomatidae (Coddington 1986a, b; Platnick & Shadab 1978; Platnick & Forster 1989; Shinkai 1989, 1990).

In summary, it is very likely that *A. simoni* measures distances moved along lines. These distances during sticky spiral construction are larger relative to the spider's size in this species, and are thus likely to be measured less precisely in absolute terms. It is interesting to note that this likely influence of Weber's law on *A. simoni* suggests that their equal precision in sticky spiral spacing (Eberhard 2007) may have been achieved despite possible disadvantages in sensing important guiding stimuli. It thus implies that the equal precision that they showed constitutes stronger evidence against the size-limitation hypothesis than was previously appreciated.

Loss of the temporary spiral. The lack of a temporary spiral in the webs of the smallest species, *A. simoni*, was counted as evidence in accord with the size-limitation hypothesis. This argument is weakened, however, by the existence of a likely alternative interpretation: the temporary spiral may have been lost in anapids because of the advantage of laying sticky lines above the plane of the orb during sticky spiral construction. In an orb without a temporary spiral, the spider can walk along under radii during sticky spiral construction (as all orb weavers do) and periodically attach sticky lines to 'upper radii' that are above the plane of the orb; if there were temporary spiral lines in the orb, the upward-directed sticky lines would be snagged on them as the spider attempted to lay them after moving to the hub (Eberhard 1987b).

Some contradictions of the size-limitation hypothesis are relatively strong

The ability of *A. simoni* to maintain a consistent correlation between the number of upper radii and the number of sticky lines attached to these lines would seem to be relatively demanding, and may involve memory. The sticky lines above the orb are laid as part of sticky spiral construction in the orb. During construction of sticky spiral lines in the planar orb, the spider goes out a radius to attach the sticky line, returns to the hub, goes out the next radius, and so on (Fig. 6b). Construction of the sticky lines above the orb plane occurs up to 5–10 min after the last radius is laid (both the upper radii and the radii in the plane of the orb are laid at the same stage of web construction) (Eberhard 1987b). A sticky line above the orb plane results when the spider returns to the hub and then climbs up an upper radius instead of onto the next radius in the orb plane.

Because anapids always walk under the radial and hub lines during the process of laying the sticky spiral in the plane of the orb (Eberhard 1987b) (as is typical of all orb weavers), the spider cannot sense the radii above the plane of the web by touching them while it is building the sticky spiral. At the moment when the spider begins to climb upward from the hub on an upper radius, it could possibly sense other upper radii, but this contact could only occur after the decision to lay a sticky line above the orb plane is made (instead of continuing to move onward in the orb proper). Spiders never gave any behavioural sign of attempting to sense these radii at this time; they never paused or tapped other upper radii (Eberhard 1987b, unpublished data). Similarly, the spider was not in position to touch sticky lines already laid above the orb plane, and also could not use the final sticky spiral in the orb as a guide,

because the last sticky line above the orb was always laid substantially prior to termination of the sticky spiral in the orb (Fig. 1). In summary, the spider probably could not sense directly either the upper radii or the sticky lines above the orb while laying the sticky spiral.

The correlation between numbers of upper radii and sticky lines could be the result of a delayed response to the stimulus (unknown at present) that triggered construction of a given number of radial lines above the orb. If this stimulus is related to the availability of points of attachment above the orb plane, the correlation would involve memory. It could also result from memory of the number of radii that the spider had laid above the orb plane during radius construction and of the sticky lines already laid above the orb plane. Other possibilities involve less elaborate memories; for instance, the stimulus that elicits more upper radii might lower the threshold for deciding to go out an upper radius to attach loops of sticky line, or decrease the distance from the hub at which the spider ceased laying sticky lines above the orb. Present ignorance of the cues involved precludes further speculation. Both construction of sticky and nonsticky lines above the orb proper, and the ability to adjust their numbers to each other are derived traits in orb weavers, because construction of planar orbs is plesiomorphic in orbicularians (Griswold et al. 1998; Lopardo et al., in press).

The ability of *A. simoni* to adjust the slope of the orb portion of the web on the basis of the space available also seems likely to be behaviourally demanding. Many orb weavers apparently judge the size and shape of the space available in which to build (Ades 1986; Vollrath 1992; T. Hesselberg, unpublished data; G. Barrantes & W. G. Eberhard, unpublished data). Although the specific cues they use are not currently known, it is likely that they integrate information on distances and directions travelled during preliminary exploration behaviour (Vollrath 1992). Path integration of the type seen in other animals (Shettleworth 2010) may be combined with a memory that allows summation of this information. Estimating the volume of open space from information of this sort is not an obviously simple mental feat, however (at least it would be a challenge for a blind-folded human). Using such information to make appropriate modifications of the orb design in the third dimension has no clear equivalent in planar orbs. As noted above, constructing three-dimensional orbs is a derived trait (Griswold et al. 1998), so presumably the ability to make these adjustments in the third dimension is also derived. Construction of orbs with sticky and nonsticky lines in the third dimension is widespread in the other 'symphytognathoid' relatives of anapids, where it apparently evolved once in the common ancestor (Lopardo et al., in press). Symphytognathoids are all very small and include the smallest species of spiders known.

It could be objected that this comparison is not fair, because one cannot expect adjustments in the third dimension from spiders that build only two-dimensional orbs. But at a larger, evolutionary scale, if small size were associated with behavioural limitations, then three-dimensional orbs (and their associated problems and opportunities for flexibility) might not have evolved in these very small spiders. The abilities of the small spiders to deal with adjustments in the third dimension represent additions to the behavioural repertoire of larger, typical orb weavers.

Still another derived trait of the smallest species that may be behaviourally challenging is the alternative 'orb sector' web of *A. simoni* (Fig. 1b). The orb sector webs are not simply mistakes: they were uniform in design and no intermediate forms were seen. Their design implies that frame, radius and hub construction behaviour were all modified. No analogous alternative prey capture webs are known in *L. mariana*, *A. bifurca* or *M. duodecimspinosa*, and such alternative designs of prey capture webs are very unusual among orb-weaving spiders in general. The only two analogous alternative

designs I know of occur in distantly related species, the small theridiosomatid *Wendilgarda galapagensis* (Eberhard 1990a) and the moderately sized uloborid *Philoponella oweni* (Eberhard 1969). Lack of alternative webs is plesiomorphic in orb weavers (Griswold et al. 1998), so the alternative orb of anapids is also derived.

Radius lengths versus inter-radial angles

The decision to limit my analyses of radius length and inter-radial angles to intraspecific comparisons might seem to deprive the size-limitation hypothesis of an apparent confirmation (compare *M. duodecimspinosa* with *A. simoni* in Table 6). But this correlation is complicated by the fact that different types of radii are laid with different behaviour patterns. During the process of building the later 'secondary' radii, an orb weaver adds each new radius adjacent to an 'exit' radius that is already present in the web, moving along the exit radius from the hub to the edge of the web where it will attach the new radius (Hingston 1923; LeGuelte 1966; Eberhard 1972; Vollrath 1992; Shinkai 1996; Zschokke 1996). The angle between these two radial lines is presumably under the spider's direct control; it is determined by how far the spider moves laterally away from the exit radius along the frame line before attaching the new radius (Hingston 1923; Peters 1937). Earlier 'primary' radii, however, are laid during and prior to the process of primary frame construction, and the behavioural processes determining their sites of attachment (and thus the angles between them) do not involve contact with the radii that will be adjacent to them in the finished orb. There are only a few radii in the orbs of *A. simoni*, and most of them end directly on the substrate, so most are probably primary rather than secondary radii. In contrast, most of the radii of the other species of this study are secondary (Eberhard 1990b, unpublished data; Vollrath 1992). Thus, I did not make interspecific comparisons, but only intraspecific comparisons of adults versus small nymphs; these showed no differences. Similar comparisons between adults and nymphs of the araneid *Eustala illicita* also showed no differences (Hesselberg 2010).

The function of the correlation between the numbers of radii and sticky spiral loops is not certain, but the function of the correlation between radius length and inter-radius angle seems clear. Longer radii separated by a given angle will be farther apart at their distal ends; by reducing the angles between longer radii, the spider will avoid having large areas near the edge of the web that lack the support and the prey-stopping abilities provided by radii (Hingston 1923; Peters 1937).

Limitations of measurements and conclusions

I assumed that greater scatter around a regression line indicated poorer, less precise behavioural performance, but this may not be true, as noted above. The fact that the spiders did make significant adjustments between variables, such the numbers of radii and sticky spiral loops, supports my assumption but does not prove it. A similar possible problem in the analysis of consistency in sticky spiral spacing (Eberhard 2007) is the assumption that the spiders indeed 'attempt' to make uniform spaces between loops of sticky spiral. The general uniformity of spacing, especially within a given area of the web, supports but does not prove this assumption.

Another possible limitation concerns the argument made to justify my attempts to measure complexity ('If species A and B execute all the same behavioural patterns with the same apparent precision, and species B in addition performs other behaviour patterns never performed by species A …'). Even though other authors have made similar arguments (Cole 1985), they are nevertheless weak. All other things are not always equal (for instance, the smaller spiders lack a behaviour, temporary spiral construction, present in larger spiders), and there is at present no information on their many other behaviour patterns, such as prey attack, web site

selection and courtship. Thus, neither the lack of a temporary spiral in the smallest species (supporting size-limitation predictions), nor the additional abilities to build alternative web forms or to adjust the number of sticky lines to the number of radii above the orb (contradicting the size-limitation predictions) constitute conclusive evidence regarding the size-limitation hypothesis.

Finally, the arguments for relating brain size to behaviour in the Introduction also have clear limitations. There is basically no experimental evidence concerning which nervous structures and mechanisms serve to control and execute orb web construction. Use of the volume of the entire brain rather than only the portions directly involved in web construction weakens the attempts to relate behavioural capabilities and brain size. In addition, relatively small amounts of nervous tissue can be sufficient to perform relatively sophisticated tasks (Chittka & Niven 2009). For instance, few differences among a set of only five stridulatory interneurons are necessary to generate sharp differences in calling and courtship songs of male grasshoppers in different genera (Ocker & Hedwig 1996). A brain of only 302 neurons in the nematode *Coenorhabditis elegans* is capable of associative learning (Zhang et al. 2005) (as well as all of the other behavioural tasks of this animal!). Modelling with neural networks also indicates that cognitive tasks can be performed with very few neurons (Chittka & Niven 2009). It seems likely that there is at least a general relationship between brain volume and behavioural abilities, but it may be weak. The fact remains, however, that the results of the present study show that very small spiders do not appear to have behavioural deficits, whatever the relationship of these behaviour patterns with brain tissue may be.

General Conclusion and Possible Evolutionary Consequences

If anything, the evidence against the size-limitation hypothesis is stronger than might be suggested by the summation of 'seven against as compared with three in favour' (Table 6). Rejection of the size-limitation hypothesis would leave the 'oversized brain' and the 'neural tricks' hypotheses as possibilities. The data in this study do not allow a choice between these ideas, which in any case could both occur in the same animals. The brains of some of the smallest spiders of this study are relatively large, thus supporting the possibility that the smaller spiders have 'oversized' brains. These data concern only the total volume of the brain, rather than that of specific portions that are involved in different behavioural abilities, and are thus difficult to interpret.

The general failure of the predictions of the size-limitation hypothesis in orb-weaving spiders does not mean that the hypothesis is not true for other groups. Perhaps the effects of reduced behavioural capacities on foraging success have a greater influence on the fitness of these spiders than similar reductions would have on the fitness of other animals whose foraging success depends on other types of behaviour. I see no easy way to test this idea except with further data. Nor does the failure of the size-limitation hypothesis in this group mean that the logic of the arguments on which it was based is incorrect. The basic question is not theoretical, but rather empirical: do very small animals tend to sacrifice their behavioural capacities because of allometric constraints on the relative sizes of their nervous systems? The answer, at least for the orb construction behaviour of orb-weaving spiders, seems to be 'No'. Examination of other behaviour patterns in these species and of the behaviour other groups will reveal whether this 'No' answer is typical of other types of behaviour and other animal groups.

If very small orb-weaving spiders maintain comparable behavioural capacities by having relatively large brains, there may be important evolutionary consequences. Conserving behavioural

capabilities in young nymphs presumably improves their abilities to forage successfully. But the costs of supporting proportionally large amounts of nervous tissue in early nymphs, in combination with the possibly reduced availability of prey that are small enough to be captured, may impose a lower limit on egg size. The relatively larger eggs, lower fecundity and smaller number of instars in smaller species of spiders (Craig 1987; Head 1995) could be at least partly due to scaling problems. Of 25 prey collected from adult *A. simoni* in the field, the majority were small nematocerous flies (56%); others included ants (8%), collembolans (8%), other flies (8%) and others arthropods (20%); thus a variety of prey are available even for such small spiders. A second possible consequence of maintaining behavioural capabilities is that evolution towards smaller adult body size in spiders as well as in other groups may be limited by the greater costs of brains in smaller organisms.

Acknowledgments

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