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# SHORT COMMUNICATION

# Does allometric growth explain the diminutive size of the fangs of *Scytodes* (Araneae: Scytodidae)?

**Robert B. Suter**: Department of Biology, Vassar College, Poughkeepsie, New York 12604, USA. E-mail: suter@vassar.edu

**Gail E. Stratton**: Department of Biology, University of Mississippi, University, Mississippi 38677, USA

**Abstract.** Spitting spiders eject silk and glue from their fangs when attacking prey. The ejection is complete in less than 35 ms and involves high-frequency fang oscillations that can approach 1700 Hz. Because of Newtonian physical constraints, these oscillations, which cause the spit to be dispersed in a zigzag pattern, could not occur at such high frequencies if the fangs themselves were not very small. We hypothesized that allometric neoteny, in which the developmental rate of a structure is retarded relative to the changing overall size of the growing individual, could explain (in an ontological sense) the small fangs of adult spitting spiders. We measured the fangs, chelicerae, carapaces, and sterna of many sizes of spitting spiders, *Scytodes thoracica* (Latreille 1802a), brown recluse spiders, *Loxosceles reclusa* Fertsch & Mulaik 1940, and wolf spiders, *Varacosa avara* (Keyserling 1877), to discover whether the fangs of spitting spiders grow unusually slowly. Using sternum width as our proxy for spider size, we found that the carapaces of spitting spiders grow disproportionately fast but that the spiders' chelicerae and fangs grow at the same rate as their sterna. The growth patterns in *L. reclusa* and in *V. avara* differed both from each other and from *S. thoracica*. We evaluate these patterns and conclude that the diminutive fangs of adult spitting spiders do not constitute an instance of allometric neoteny.

**Keywords:** Spider predation, morphology, spitting dynamics, neoteny, ontogeny

Spitting spiders such as *Scytodes thoracica* (Latreille 1802a) (Araneae: Scytodidae) capture prey by entangling them in a mixture of silk and glue that the spiders eject through the venom duct in their fangs (Monterosso 1928; MacAlister 1960). The ejection is highly organized (Gilbert & Rayor 1985; Foelix 1996) and remarkably rapid. The ejected material, traveling at up to 28 m/s, forms an ordered zigzag pattern because the spider raises its chelicerae while its fangs oscillate, and an expectoration episode seldom lasts longer than 35 ms (Suter & Stratton 2009).

From a biomechanical perspective, the movement of the fangs is particularly interesting because their high frequency of oscillation (mean 826 Hz, maximum 1700 Hz) must be closely coupled to the mass of the fang, because it is the fang that must be accelerated at each extreme of its displacement. The rotational version of Newton's Second Law, tells us that

$$\tau = I \cdot \alpha \quad \text{or} \quad \alpha = \frac{\tau}{I} = \frac{\tau}{\Sigma \mathrm{mr}^2}$$

angular acceleration ($\alpha$) is the quotient of torque ($\tau$) divided by the moment of inertia ($I$), where $I$ is the sum of the products of mass and radius-squared ($\Sigma \mathrm{mr}^2$) for all particles making up the rotating structure. So, to achieve a given acceleration (and thus frequency of oscillation), as mass rises, torque must rise proportionately; or, for any given muscular or hydrodynamic torque, as mass rises, acceleration (and thus frequency of oscillation) must fall. (In the more familiar but less apt linear version of Newton's Second Law, $F = ma$, force is the equivalent of torque, acceleration replaces angular acceleration, and mass replaces the moment of inertia. In that version, like the rotational one, acceleration is directly proportional to force and inversely proportional to mass.) In this unavoidable physical context, a spitting spider with smaller fangs can achieve a higher oscillation frequency than an otherwise comparable spider with larger fangs, or can achieve the same oscillation frequency with less effort than would be expended by an otherwise comparable spider. It is not unexpected therefore to find that spitting spiders have very small fangs relative to the spiders' overall dimensions (Figs. 7–11 in Suter & Stratton 2005).

In the study reported here, we sought to test whether or not the adult spitting spider's diminutive fangs can be attributed to neoteny, the retention of juvenile traits in mature organisms. We approached this ontogenetic problem through allometry. As animals grow, the dimensions of their various parts increase, but seldom do so at the same rates. Entirely isometric growth implies that all parts grow comparably fast, so that a doubling in femur length would be accompanied by a doubling in tibia length and a doubling in the distance between the anterior median eyes. In fully isometric growth, a young animal would have exactly the same shape as an adult. Allometric growth implies that some parts grow faster than others, so that a doubling in femur length might be accompanied by a tripling of tibia length but no change at all in the distance between the eyes.

Allometric growth is usually detected by evaluating the allometric equation

$$y = bx^a \quad \text{or} \quad \log y = \log b + a \log x$$

in which $y$ and $x$ are the dimensions of two structures or other measurable properties (e.g., metabolic rate) and $a$ is the allometric coefficient. In a regression of $\log y$ on $\log x$, the slope is $a$ and the intercept is $\log b$; when $a < 1$, growth is negatively allometric, when $a = 1$, growth is isometric, and when $a > 1$, growth is positively allometric (Huxley 1932; Smith 1980; Harvey 1982).

We hypothesized that the relatively diminutive fangs of adult *S. thoracica* were the result of a negative allometry in which the fangs grew more slowly than other parts of the spider's anatomy throughout the life of the spider; this would result in adult spiders with disproportionately small fangs. To test this hypothesis, we measured fang length (tip to hinge), chelicera width (maximum), sternum width (maximum), and carapace width (maximum) in spiders that varied in size from hatchlings to adults. Carapace width is often used as a proxy for spider size (Hagstrum 1971), but we elected to use sternum width instead because the carapace of scytodids is abnormally large due to the hypertrophy of the venom glands (Foelix 1996; Ubick et al. 2005; and Fig. 6 in Suter & Stratton 2005) and so would, a priori, be an inappropriate proxy.

Because spider growth is strongly dependent on prey ingestion rate and only loosely attached to the passage of time (Homann 1949;

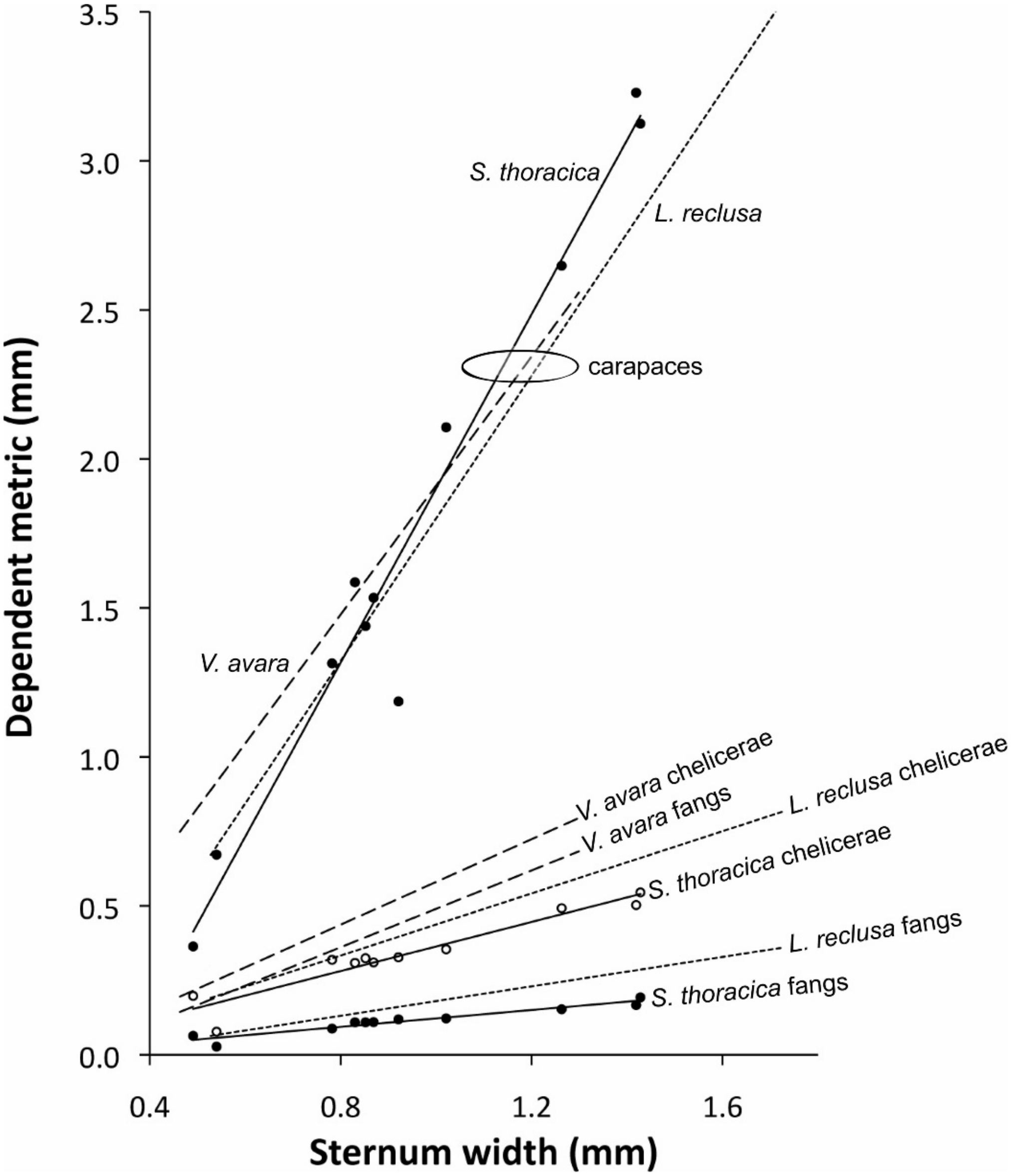

Figure 1.—Linear plots of the growth of fangs, chelicerae, and carapaces (relative to sterna) of *Scytodes thoracica* (solid circles and lines), *Loxosceles reclusa* (dotted lines), and *Varacosa avara* (dashed lines). To preserve visual clarity, data points are omitted for *L. reclusa* and *V. avara*. See Fig. 2 for the same data plotted as logarithms.

Higgins 1992, 2000; Sullivan & Morse 2004; Morse 2007), our independent variable throughout was sternum width rather than either time per se or developmental stage.

To facilitate measurement, we made calibrated images of whole spiders viewed under a dissecting microscope to get sternum and carapace dimensions, and we wet-mounted chelicerae and fangs on the stage of a compound microscope to make calibrated images of these two structures. We concentrated on three species: a spitting spider, *S. thoracica*, our focal species, collected in Oxford, Lafayette County, Mississippi; the brown recluse spider, *Loxosceles reclusa* Fertsch & Mulaik 1940 (Araneae: Sicariidae), another haplogyne species relatively closely related to the spitting spiders, collected from a variety of sites in Marshall and Lafayette Counties in Mississippi; and a wolf spider, *Varacosa avara* (Keyserling 1877) (Araneae: Lycosidae), a cursorial entelegyne spider distantly related to the spitting and recluse spiders, collected from Abbeville, Lafayette County, Mississippi.

Figure 1 shows the relationships between sternum width and the other dimensions we measured in the three species for which we collected developmental series. In each case, carapace width, chelicera width, and fang length increased approximately linearly with sternum width, our proxy for spider size. The relationships elucidated by applying the allometric equation, between the $\log_{10}$ of sternum width and the $\log_{10}$ of the other measures, varied interestingly among the three species we studied (Fig. 2, Table 1).

As expected from the spitting spider's hypertrophied venom glands and consequently enlarged cephalothorax (Foelix 1996; Suter & Stratton 2005; Ubick et al. 2005), the spitting spiders' carapaces grew with positive allometry (slope ± 95% CI = 1.90 ± 0.43, significantly greater than the isometric slope of 1.00). Their carapaces also grew more rapidly, in relative terms, than those of the brown recluse spiders (slope = 1.36 ± 0.10) and the wolf spiders (slope = 1.22 ± 0.16). In all three species, carapace growth was more rapid than sternum growth (slope $> 1.00$).

In the spitting spiders, fang and chelicera growth rates were indistinguishable from sternum growth (slope ~ 1) and were thus apparently isometric. In contrast, the fangs and chelicerae of the brown recluse spiders showed positively allometric growth rates (slopes > 1) that were not significantly different from the growth rate of the carapace. In *V. avara*, the wolf spider, the fangs and chelicerae grew with positive allometry (slopes > 1), with the fangs growing fastest.

Our hypothesis was that the fangs of adult *S. thoracica* are small because their growth was slow relative to the growth of other structures and thus relative to growth of the body as a whole. Rejecting this hypothesis would require both a) that the fangs of spitting spiders grow as fast or faster than the body as a whole and b) that we chose a suitable proxy for body size. The data (Fig. 2, Table 1) show that the fangs, chelicerae, and sternum of spitting spiders grow at the same rate (slope ~ 1), while carapace width grows markedly faster. Thus we may need to reject our hypothesis because we have satisfied one (a, above) of the necessary criteria for rejection. The data (Fig. 2, Table 1) also show that comparing the growth of other structures vs. the growth of the sternum can detect instances of non-isometric growth that are either expected (enlargement of the spitting spider's cephalothorax) or are consonant with our impressions from other studies (the large relative size of adult wolf spider's chelicerae and fangs; Rovner 1980; Walker & Rypstra 2001). This satisfies the other (b, above) of the necessary criteria for rejection.

We must, therefore, reject our initial hypothesis and accept the alternative that, although the fangs of *S. thoracica* grow slowly relative to the enlarged cephalothorax, the fangs do not grow more slowly than would be expected in isometric growth. Thus allometric neoteny, in which the developmental rate of a structure is slowed relative to the changing overall size of the growing organism (Gould 1977; McNamara 1986), cannot explain the small size of the spitting spider's fangs and we must search elsewhere for an explanation.

Because the fangs of hatchling and adult spitting spiders have the same relative size, the explanation of small fang size, even among the smallest spitting spiders, may be found in the family's phylogeny rather than in the ontogeny of the individual spiders.

Because details of that evolutionary path remain obscure, we cannot justify an assertion that the unusually small fangs of spitting spiders evolved in support of the fangs' function in ejecting spit while oscillating at high frequency. Among haplogynes, for example, the fangs of *Artema atlanta* Walckenaer 1837 (Pholcidae) are no larger relative to sternum width (unpublished data) than are the fangs of the spitting spider; because these two species are in the same clade within the Haplogynae, and the pholcids do not spit while the scytodids do, it is quite possible that small relative fang size evolved first in an ancestor shared by both species. If that is the case, then the ancestors of modern scytodids merely took advantage of the pre-existing condition while other components of spitting physiology and morphology were evolving.

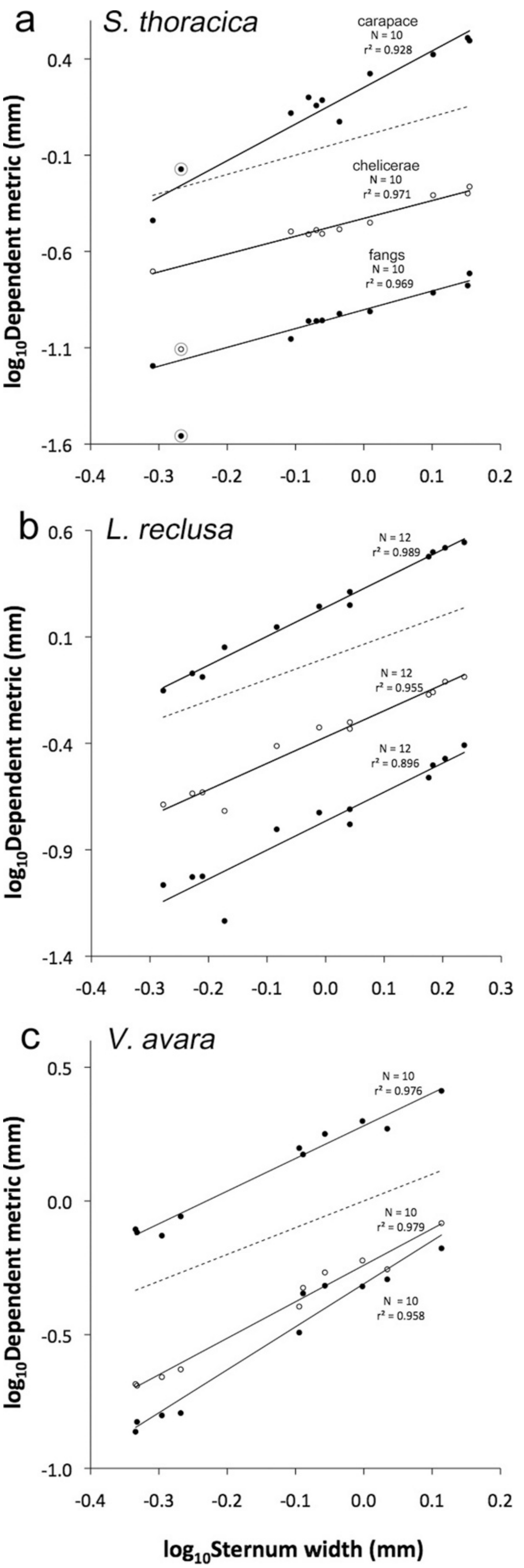

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Figure 2.—Logarithmic plots of the growth of fangs, chelicerae, and carapaces (relative to sterna) in three spiders. *S. thoracica* (a) showed significant positive allometry in the growth of its carapace, but its chelicerae and fangs grew at the same rate as the sternum. (Data indicated by large open circles are excluded from the linear fits because they are clear outliers: for the carapace and fang fits, $r^2$ improved from 0.75 and 0.79, respectively, to 0.97 for each when the outliers were excluded.) Growth rates in *L. reclusa* (b) were positively allometric relative to the sternum and the slopes of the lines for carapace, chelicerae, and fangs were not different from each other. Growth rates in *V. avara* (c) were also positively allometric, with significant slope differences among carapaces, chelicerae, and fangs. Dashed lines have slopes of 1.0. Slope analyses are shown in Table 1.

Table 1.—Slopes, slope comparisons, and 95% confidence intervals of the log-log relationships shown in Fig. 2.

| Spider | Structure | Slope | 95% CI |
|---|---|---|---|
| *S. thoracica* | Carapace | 1.901 | 1.469–2.334 |
| | Chelicera | 0.926 | 0.796–1.056 |
| | Fang | 0.976 | 0.833 to 1.120 |
| | $F_{2,24}$ | 21.388 | |
| | $P$ | $< 0.0001$ | |
| *L. reclusa* | Carapace | 1.359 | 1.259–1.460 |
| | Chelicera | 1.235 | 1.046–1.425 |
| | Fang | 1.361 | 1.035–1.688 |
| | $F_{2,30}$ | 0.507 | |
| | $P$ | 0.608 | |
| *V. avara* | Carapace | 1.221 | 1.064–1.378 |
| | Chelicera | 1.365 | 1.201–1.530 |
| | Fang | 1.607 | 1.333–1.881 |
| | $F_{2,24}$ | 4.787 | |
| | $P$ | 0.018 | |

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