MORPHOLOGY AND ALLOMETRY OF THE PURSE-WEB OF *SPHODROS ABBOTI* (ARANEAE, ATYPIDAE): RESPIRATORY AND ENERGETIC CONSIDERATIONS

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ABSTRACT

The influence of web morphology and allometry on respiration and energetics was investigated in the purse-web spider, *Sphodros abboti*. Carbon dioxide and oxygen concentrations in gas samples from underground portions of the nest where these spiders normally reside did not differ significantly from those in atmospheric air. Web dimensions such as length, diameter, and surface area scaled geometrically to body size. The scaling of these relationships differed from expected. Since the surface area of the web functions in prey detection, I anticipated it would scale in parallel with increases in energy demand that accompany size increases. Rates of oxygen consumption serve as an index of the latter and scale in direct proportion to body size whereas web surface area scales only to the two-thirds power. The weight of the web scaled to a power less than predicted by simple geometry, a result interpreted as an adaptation towards reducing costs of web construction. These results and comparisons suggest the web and its morphology do not restrict respiratory gas exchange nor limit energy acquisition in this species. Conversely, the standard rates of metabolism in this species were not higher than those of related species that also burrow but do not use a web for prey capture.

INTRODUCTION

The purse-webs of the atypid spiders found in temperate zones of North America are tubular structures attached vertically to the sides of hardwood trees (Gertsch and Platnick 1980). These webs extend above and below ground with the spiders normally residing in the subterranean portion. The aerial part of the web serves to alert the resident spider of potential prey walking or landing on its surface. The alerted spider proceeds upward within the web and attacks the prey through the web with long fangs. Once immobilized, the prey is pulled through a slit in the web and eaten.

This type of web can be considered as an extension of the silken lining of the spider's burrow into the aerial environment. Nentwig and Heimer (1983) suggested that evolution of webs extending above ground level allows for more effective prey detection and capture. Increased prey capture may permit increases in rates of energy expenditure thus increasing rates of growth and reproduction (Anderson 1970; Anderson and Prestwich 1982). If this interpretation is correct, one should be able to detect and correlate differences in standard rates of metabolism between atypid spiders and other tarantulas that do not use webs for prey capture. My aim was to make such a comparison. I selected *Sphodros abboti* Walckenaer for study as it is common in mesic hardwood habitats in north Florida.

The nature of the web in atypid spiders complicates interpretation of such comparisons. The gas composition within the underground portion of the web may differ significantly from atmospheric air and therefore rates of metabolism may be under selective pressures in addition to those assumed to be operating. These spiders spend virtually all of their lives within the web. Soil particles and other debris are incorporated into the wall of the tubular web (Gertsch 1979; Gertsch and Platnick 1980; Coyle and Shear 1981) during construction. Living material such as mosses are passively incorporated within the web, particularly those of older individuals. Underground, where the spider normally resides, the walls of the silken tube are thicker than in aerial portions (Coyle and Shear 1981). These spiders construct their nests in moist sandy soils with a high humus and loam content. The ground is usually covered by a continuous layer of leaf litter. Restricted gas exchange, decomposition of organic matter, high water content in these soils, and respiration of symbiotic organisms and spiders may promote hypercarbic and hypoxic conditions within the burrow (Levy and Toutain 1982) and thus affect their rates of metabolism (Withers 1978; Tanaka and Saito 1984). I believed it necessary to measure O_2 and CO_2 levels within the bottom of the purse web to provide a more valid interpretation of their rates of metabolism.

An additional aim was to determine the relationship between size of the web and size of the spider. Coyle and Shear (1981) reported that web size is a function of body size and conditions at the nest site. The web serves as a nest for the entire life of the individual spider and is enlarged to accommodate growth. Since energy demands increase with increases in size, one would expect web size to reflect these demands. A similar question has been evaluated in mammals (Harestad and Bunnell 1979; McNab 1983) and other vertebrates (Peters 1983; Calder 1984). Home range has been used as a measure of the minimum size necessary for obtaining the energy required to support the organism. Its relationship to body size has been determined for a large number of vertebrates (Peters 1983; Calder 1984) and compared to metabolism-body weight regressions to provide a more complete understanding of their ecological energetics.

Although the energetic constraints appear important in determining territory size and other relevant variables in some spiders (Kronk and Riechert 1979; Riechert 1974, 1978), no comparisons have been made of metabolism and web size regressions. My aim was to explore these relationships in *S. abboti*. Previous reports (Anderson and Prestwich 1980, 1982) indicate that morphological parameters of the book-lungs of spiders do not scale to maintain geometric similarity (isometric scaling) as spiders increase in size, but exhibit increases consistent with metabolism-body size regressions. As such, I anticipated that the surface area of atypid webs would scale in parallel with increases in rates of metabolism as these animals increase in size.

An alternative hypothesis involves consideration of the costs of web production. If larger web size does increase the efficacy of prey capture, spiders should produce very large webs. However, as many have suggested (Lubin 1973; Denny 1976; Nentwig 1983; Nentwig and Heimer 1983), selective pressures would operate towards reduction of these costs. Here I would expect web parameters to increase isometrically for a given web shape with all characteristic linear dimensions (L) of the web scaling to the one-third power of body mass, surface area (L^2) scaling to two-thirds power of body mass, and volume or weight of the

web (L^3) scaling in direct proportion to body mass. Since the major cost of web production is its mass (Prestwich 1977), I also planned to obtain the data necessary to determine its scaling relationship with body size.

METHODS AND MATERIALS

Animals.—Specimens of *S. abboti* were collected from Florida State Parks at Ichetucknee Springs, Suwannee County, and O'leno, Columbia County. Selection of specimens was made from the size of their webs taking care that a representative sample of body sizes was collected. The specimens were obtained by removal of the soil surrounding the underground portions of the tube webs and then cutting any of the latters' attachments to trees. The webs containing the resident spiders were transported to the lab.

Rates of metabolism.—Rates of oxygen consumption (μL O_2/hour, STPD, at 20^{0}C) for individuals over the size range found in this species were obtained from a previous study (Anderson and Prestwich 1982). I selected 20^{0}C as it represents, on an annual basis, an average thermal environment for this long-lived species in north Florida. These rates were determined using a Gilson Differential Respirometer following the procedures reported earlier (Anderson 1970).

Burrow gas composition.—The air within the below-ground portions of the purse-webs was analyzed for oxygen and carbon dioxide using a Scholander 0.5 cc Gas Analyzer (Scholander 1947). A 1.0 cc glass syringe with attached 3-way valve, syringe needle and length of catheter tubing (PE-90) was used to obtain gas samples. The catheter tubing was inserted through a small hole in the web at ground level and slowly pushed to the bottom of the burrow. A 1.0 cc sample was taken and partially ejected via the 3-way valve to clear the dead space of the sampler. The remainder was immediately analyzed for O_2 and CO_2 dry gas composition. These determinations were made in the field with only a short delay of a few minutes between collection and analysis of samples. Comparisons of analysis of atmospheric air (N = 10) with known values indicated average deviations of +0.03% (SE $\pm$ 0.004) and −0.17% (SE $\pm$ 0.15) for CO_2 and O_2, respectively.

Morphological measurements.—Webs were slit open to extract the spiders. Specimens were weighed to the nearest mg or, in the case of the smaller animals, to the nearest 0.1 mg. All were returned to where captured and released. Their webs were used either for measurements of their dimensions or cleaned and dried prior to determination of their weight. Webs were mounted flat on paper, taking care to avoid stretching, and traced. Measurements included length of web, diameter at ground level, and surface area. The latter was determined using a polar compensating planimeter. Webs were washed repeatedly with agitation to remove, as much as possible, humus soil particles, and other extraneous material. They were dried at 105^{0}C to a constant weight.

Data analysis.—Rates of oxygen consumption and web measurements were related to body size by regression analysis. I used live body mass (in milligrams) as an index of size. As Günther (1975) and Calder (1984) both emphasize, body mass is the most appropriate measure of size in most animals. Since most regression studies indicate physiological and morphological variables do not increase in direct proportion with increases in body size (Peters 1983; Calder

Table 1.—Composition of gas in the burrow of *Sphodros abboti*.

VARIABLE	N	$\bar{x}$	SE	RANGE
Depth of Sample	8	8.4 cm	1.3	3.9 - 14.0 cm
Percent CO_2	8	0.25	0.04	0.15 - 0.50
Percent O_2	8	20.62	0.03	20.50 - 20.73

1984; Schmidt-Nielsen 1984), I fitted my data to the power function $Y = aM^b$. Here Y is the parameter in question in relation to size, M; a is a proportionality constant characteristic of the particular group of organisms; and b is the exponent of the function that describes the effect of size on the variable. The parameters, a and b, were calculated by least squares analysis of the paired data after transformation to common logarithms. I followed the recommendations of Peters (1983) and Smith (1984) and calculated the standard error (Sb) and 95% confidence limits for b, r^2, and Sy·x as indices of fit for each regression.

RESULTS AND DISCUSSION

The concentrations of CO_2 and O_2 in burrows of *S. abboti* are reported in Table 1. Comparison with given values and measured values (in %) for CO_2 and O_2 in atmospheric air (0.03 and 20.95 and 0.06 and 20.78, respectively) indicates these animals experience only mild hypercarbia and hypoxia while in their nests. These burrow concentrations are not as different from atmospheric air as are those found in termite nests (Lee and Wood 1971) and the deeper burrows of tiger beetle larvae (unpublished data). Since CO_2 and O_2 levels in the burrows of *S. abboti* do not approach those reported to affect respiratory processes in spiders (Dresco-Derouet 1960; Tanaka and Saito 1984), I do not believe they are important in affecting their rates of metabolism and could be eliminated as a consideration in my analysis.

I compared rates of metabolism of *S. abboti* with those reported for theraphosids (tarantulas) to determine whether this parameter is correlated with use of webs in prey capture. Although tarantulas live in natural cavities or make burrows whose upper regions are lined with silk, most do not use this material to construct devices to capture prey. I calculated a regression using the available data (Anderson 1970; Dresco-Derouet 1971, 1972, 1973; Greenstone and Bennett 1980) for use in predicting rates of metabolism for *S. abboti* of adult size. The regression included data from 13 species ranging in size from 142 to 36,000 mg. It predicts a rate of metabolism of 28 μL O_2/h for an individual weighing 500 mg; this predicted value is equal to that observed for adults of this species. This similarity suggests rates of metabolism in *S. abboti* are not correlated with use of a web. This conclusion should be considered tentative until additional data from other related species becomes available for comparison. One problem of using theraphosids for comparison is that most species are much larger than *S. abboti*, thus complicating the analysis. Unfortunately rates of metabolism of other related spiders of similar size, e.g., trap-door spiders (Ctenizidae), are not available.

The parameters of the regressions describing relationships between rates of metabolism and web measurements to live body mass are reported in Table 2 and shown in Figs. 1-5. The metabolism and web weight regressions include outlying

Table 2.—Relationships of oxygen consumption and web morphology to body mass in *Sphodros abboti*.

RELATIONSHIP	N	RANGE IN BODY MASS (mg)	$Y = aM^b$					
			a	b	Sb	95% CL for b	r^2	Sy·x
$\dot{V}O_2$ at 20°C (μL O_2/h)	18	22 - 625	0.082	0.94	0.039	0.86 - 1.02	0.97	0.053
Web Weight (mg)	20	0.7 - 715	8.8	0.74	0.040	0.66 - 0.82	0.95	0.118
Web Length (cm)	29	7.9 - 577	3.72	0.38	0.030	0.32 - 0.44	0.85	0.089
Web Diameter (cm)	29	7.9 - 577	0.18	0.31	0.021	0.27 - 0.35	0.89	0.061
Web Surface area (cm^2)	29	7.9 - 577	2.37	0.65	0.038	0.57 - 0.73	0.92	0.110

values at lower body size (Figs. 1 and 2, respectively) and I was concerned they might bias these relationships. Recalculation after exclusion of the outlying values resulted in insignificant changes in slope values; from 0.94 to 0.90 and from 0.74 and 0.71 for the metabolism and web weight regressions, respectively. Inclusion of extreme values decreases the standard errors of the slopes (Sb) from 0.063 to 0.039 and from 0.058 to 0.040, respectively, thus supporting the view that these equations, as given in Table 2, are valid estimates of these relationships.

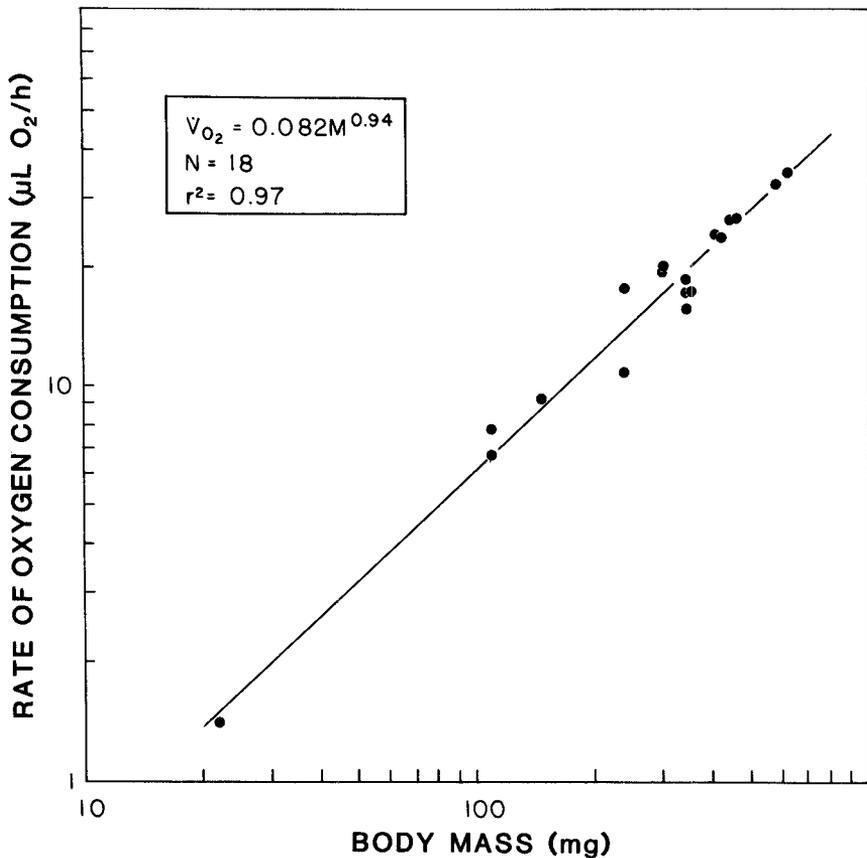$$V_{O_2} = 0.082M^{0.94}$$
$$N = 18$$
$$r^2 = 0.97$$

Fig. 1.—Relationship between rates of oxygen consumption and live body mass in *Sphodros abboti* at 20°C.
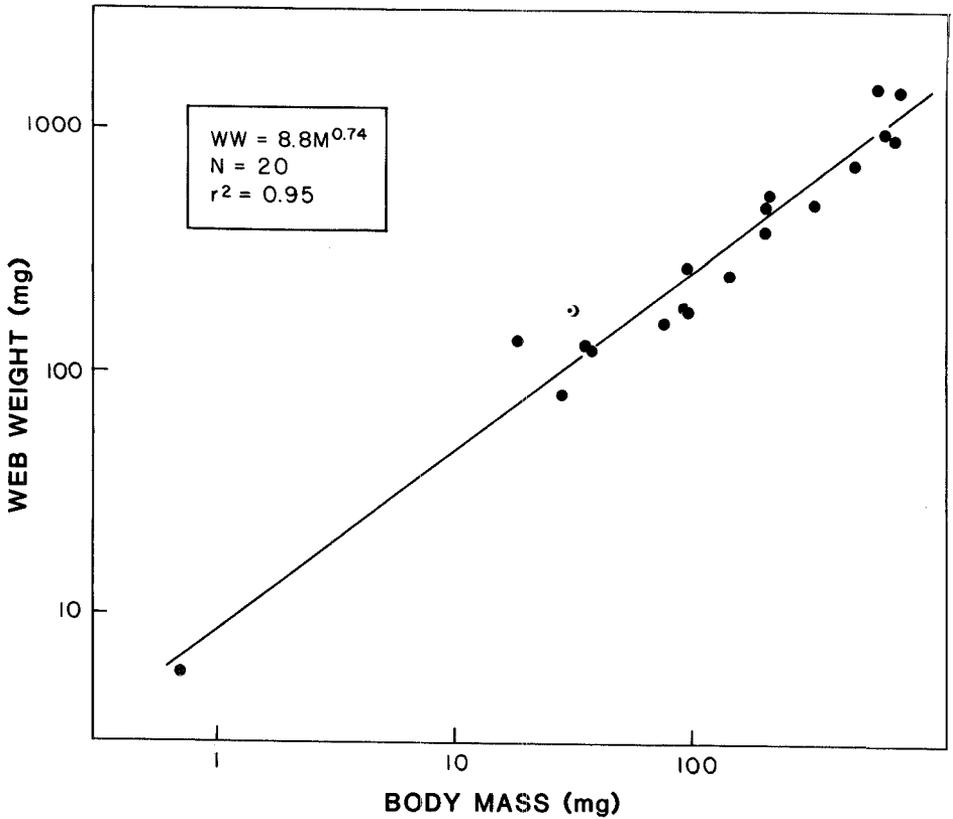
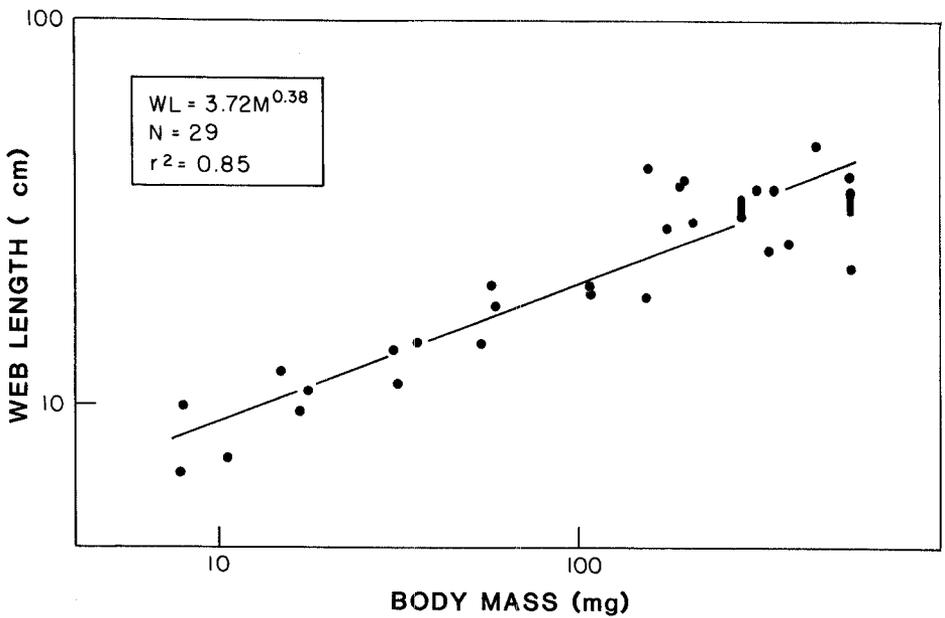Fig. 2.—Relationship between web weight and live body mass in *Sphodros abboti*.

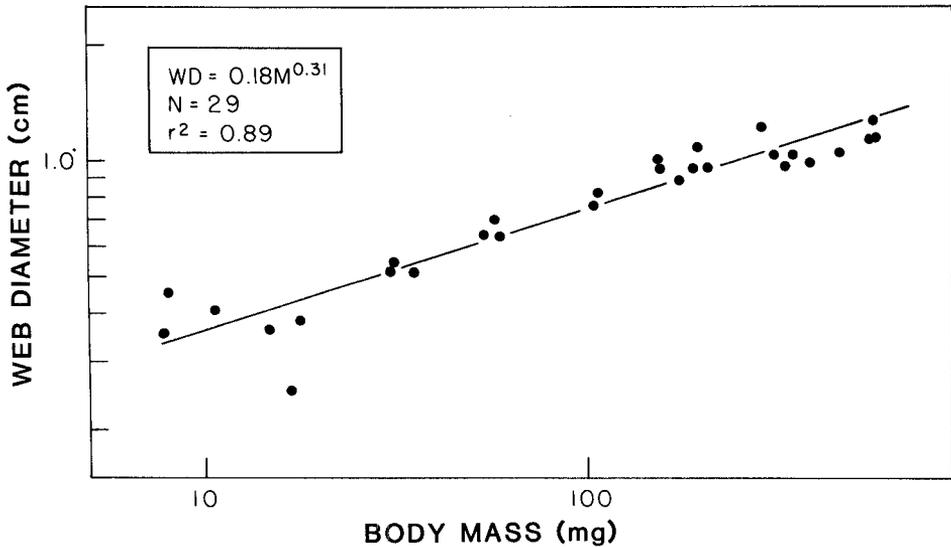Fig. 3.—Relationship between web length and live body mass in *Sphodros abboti*.

Fig. 4.—Relationship between web diameter and live body mass in *Sphodros abboti*.

The regressions relating length, diameter, and surface area of the web to body mass (Table 2, Figs. 3, 4, and 5) indicate they scale isometrically. The slopes of each equation do not differ significantly from those predicted for geometrically similar structures of different size where web length and diameter scale to the one-third power of body mass ($P = 0.11$ and 0.35, respectively) and surface area scales to the two-thirds power of body mass ($P = 0.60$).

This was an unexpected result. Although the isometric model is frequently used for such comparisons, isometric scaling is not commonly observed (Schmidt-Nielsen 1984). Departures from isometric scaling have been documented for respiratory and circulatory parameters in spiders (Anderson and Prestwich 1980, 1982) with the deviations in a direction consistent with meeting demands for respiratory gas exchange and transport. Consequently I expected the surface area of the web would scale to body size in parallel with scaling of rates of metabolism. I did consider the possibility that the surface area of only the aerial portion of the web might scale differently from that of the entire web as it is the former that is involved in prey detection and capture. Calculation, however, yields an equation whose slope and confidence intervals are almost indistinguishable from those obtained for the surface area equation listed in Table 2.

A comparison with the regression describing the relationship between rates of oxygen consumption and size in *S. abboti* is germane to the goals of this study. The scaling exponents of web surface area and oxygen consumption regressions are significantly different from one another ($P = 0.003$). The increase in surface area and presumably its effectiveness in prey capture does not increase as fast as do rates of metabolism during ontogeny in this species. For a ten-fold increase in body size, the demand for energy or rates of metabolism increase about nine times (antilog $0.94 = 8.7$) while surface area increases only 4.5 times (antilog $0.65 = 4.5$). A number of studies have related web parameters to body size in orb-weaving spiders (Howell and Ellender 1984 and citations therein). Although the nature of their data precludes complete regression analysis, it does indicate that the web surface area to body size ratios decrease with increases in spider size. In
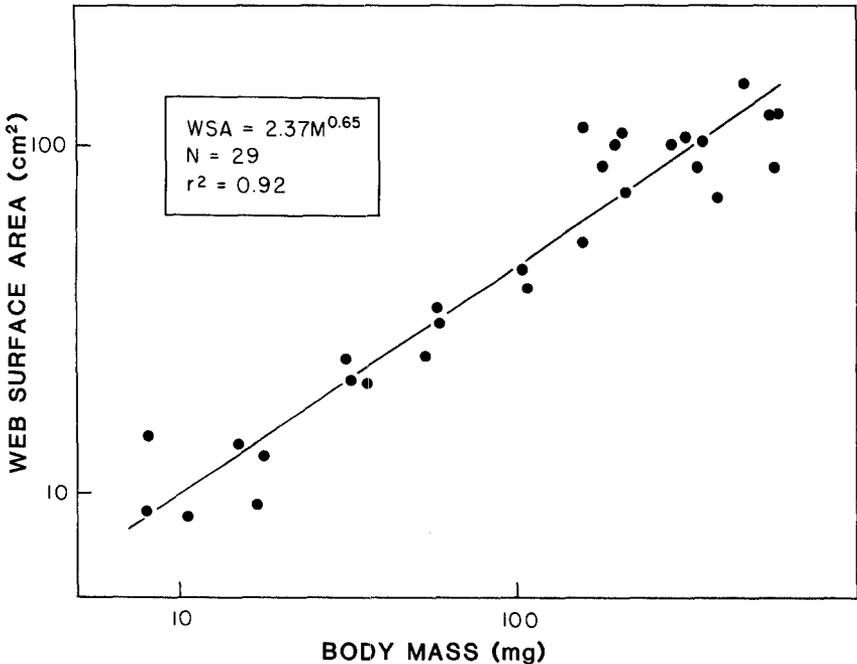
Fig. 5.—Relationship between web surface area and live body mass in *Sphodros abboti*.

araneids, as in *S. abboti*, metabolism scales in direct proportion to body size (Anderson and Prestwich 1982).

These results suggest the web of *S. abboti* and possibly other spiders are not limiting in their ability to capture prey in amounts required to support metabolic requirements. Obviously adult *S. abboti* are successful in obtaining enough energy to maintain themselves for years in this long-lived species. Of significance here is the observation that the European atypid of similar size to *S. abboti*, *Atypus affinis* Eichwald, builds a very short aerial web, about 20% of total tube length (Locket and Millidge 1951). In *S. abboti*, the length of the aerial portion is about 67% (Coyle and Shear 1981; this study). This comparison also suggests that web size is not energetically limiting in atypid spiders.

This situation differs from that found in mammals where home range scales to a higher power of body mass than do rates of metabolism (Harestad and Bunnell 1979). Although the reasons explaining this difference between the two relationships in the direction indicated are not completely known (McNab 1983), most discussions involve energetic considerations. The difference between spiders and mammals may serve to emphasize the adaptive significance of the low rates of metabolism in spiders (Anderson 1970; Greenstone and Bennett 1980; Anderson and Prestwich 1982). Most spiders have rates of metabolism about 50% lower than those of other poikilotherms of comparable size. The difference between observed and expected rates of metabolism is even larger in adult *S. abboti* with females exhibiting rates only 34% expected for their size (Anderson and Prestwich 1982). This reduced level of metabolism may provide freedom from energetic constraints (Greenstone and Bennett 1980) and represents an adaptation to buffer fluctuations in food availability. To put this adaptation into a more meaningful context, I calculated that an adult *S. abboti* (500 mg), at a rate of

metabolism predicted using the appropriate equation (Table 2), would have to eat its weight in insect tissue only once about every 170 days to remain in energy balance. Even if completely unsuccessful in obtaining prey, they would not succumb to starvation until after 200 days or more. Data used to make these estimates such as energy content of insect tissue, ingestion efficiency, etc., were obtained from various sources (Golley 1961; Anderson 1974; Riechert and Tracy 1975).

This adaptation would allow these spiders to reduce the cost of web construction without compromising effectiveness of prey capture. Since most of the cost in web production is in the amount of silk used (Prestwich 1977), savings would accrue if the larger webs of adults used smaller amounts of silk than required by web design features. One can predict how web weight would scale to body mass from the product of the regression equations relating surface area and length of the web to body mass, i.e.,: web weight is proportional to web surface area x web length. Using the weight exponents for each of these expressions (Table 2) indicates web weight should scale in direct proportion to body mass. This is not the observed result (Table 2, Fig. 2). Web weight scales to a power significantly less than one, the predicted value, (b = 0.74, $P \lll 0.001$). This difference between expected and observed is explained by the observation that the thickness of the silken tube decreases in the aerial portion of the tube web (Coyle and Shear 1981). I suggest the departure from proportional scaling of web weight is an adaptation to reduce costs (and possibly conserve amino acids) in web construction.

Although the data and analysis have emphasized energetic considerations, I believe the tubular web of *S. abboti* is the result of a complex evolutionary history and therefore subject to selective constraints in addition to those involving energy. Obviously such constraints need further study to fully understand the functional advantages of this type of web.

ACKNOWLEDGMENTS

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