

Energetic cost of web construction and its effect on web relocation in the web-building spider *Agelena limbata*

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Summary. Although spider webs may be effective in trapping prey, they require energy for construction. The design of webs varies in complexity from species to species. I assume that the energetic cost of web construction is significantly different among web types or species. This cost may constrain foraging tactics, particularly web relocation, because web relocation also requires energy to make a new web. To clarify the effect of the cost of web construction on web relocation, the energy cost of web construction and the rate of web relocation were estimated for the spider *Agelena limbata*. This spider constructs a sheet-funnel web consisting of a tight mesh of silk threads. This web was costly in terms of the energy needed for construction, which ranged from 9 to 19 times the daily maintenance energy. The daily rate of web relocation was below 1%, indicating high web-site tenacity. Relocation rates of species which built different types of web were compared in relation to cost of web construction. Orbweavers, which produce less costly webs than sheet-funnel weavers, relocate webs more frequently. Sheetweavers, which make webs of intermediate cost, appear to relocate webs more frequently than sheet-funnel weavers but less frequently than orbweavers. These results suggest that the energy cost of web construction is important in determining the frequency of web relocation.

Key words: Energetic cost – Web construction – Web relocation – Spider

Spider webs may be effective prey traps but require energy for construction. Some spiders build very simple webs that consist of a single or a few lines of silk, but others make rather complex webs. One would expect that the energetic cost of web construction would vary notably among web types, depending on the amount of silk used and activity necessary for construction.

Profitability of web sites affects survivorship and reproductive success in spiders (Riechert and Tracy 1975; Riechert 1981). Parameters of web-site quality, such as prey availability, may vary spatially and temporally. Spiders can

respond to variation in web-site quality by leaving the site and reconstructing a web at another site (Turnbull 1964; Olive 1982). Web relocation, however, requires energy expenditure. I assumed that the major cost of web relocation would be the energy involved in constructing a new web, and hypothesized that the energy cost of web construction would affect the decision as to web relocation; more specifically, spiders that construct more costly webs should relocate the webs less frequently. A few authors have reported the rate of web relocation in orbweaving spiders (Eberhard 1971; Enders 1975; Janetos 1982). Orbwebs consist of a rather sparse mesh of silk threads and, thus, require a small amount of silk. Data on web relocation of spiders that produce more costly webs are lacking, except for a study on sheetweavers by Janetos (1982).

The web of *Agelena limbata* Thorell (Araneae: Agelenidae) is not adhesive and consists of a flat sheet, funnel retreat, and barrier web. The barrier web is an irregular network of silk strands which serves to knock down the flying insects onto the sheet or to prevent prey from escaping. The sheet and funnel are characterized by a very tight mesh of silk threads and may require much silk. This feature suggests that the web of *A. limbata* is costly in terms of energy for construction. If true, I predict that this spider will be tenacious on its web site. This paper estimates the energetic cost of web construction and the rate of web relocation in *A. limbata* and provides evidence to support the hypothesis by comparing several types of web builders.

Materials and methods

Spiders

Egg sacs of *A. limbata* were collected in the experimental field of Nagoya University in September 1983. The spiderlings emerged from the egg sacs the following spring. These spiderlings are defined here as instar 1 although they undergo the first molt within the egg sac. The spiders were reared individually from instar 1 to adults in plastic containers of appropriate size under 25°C, 16L:8D. The spiders built webs including the sheet and funnel in these containers. The spiders were supplied ad libitum with *Drosophila melanogaster*, *Musca domestica*, larvae of *Spodoptera litura* and nymphs of *Blattella germanica* every 2 or 3 days. Water was also provided by a hand sprayer.

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Determination of energetic cost of web construction

The net energetic cost of constructing a web, C_w (cal), can be calculated according to the following equation:

$$C_w = (A + S)W_w$$

where A is the metabolic increment for activity of web-spinning, expressed as cal per unit weight of web (cal/mg), S is the calorific equivalent of web silk (cal/mg) and W_w is the total weight of a web (mg). The metabolic increment for activity (A) is defined as metabolic rate during web construction minus standard metabolic rate.

The metabolic rate was determined by measuring the oxygen consumption rate with a Shimadzu GC-8APT gas chromatograph equipped with a thermal conductivity detector (Shimadzu Corporation, Kyoto, Japan) and a Shimadzu C-R1B data analyzer (for details, see Tanaka and Saito 1984). The spiders were acclimated to the experimental temperatures of 15°, 20°, and 25° C for 5 days prior to the measurement, being deprived of food but not water. Standard metabolic rates were measured using four sizes of glass vials (1.0, 2.3, 7.0, 11.5 ml) as respiratory chambers, according to spider size. The inside surface of the vial was covered with nylon gauze to mimic the web. Spiders settled down and spider activity was minimized. The spider was introduced into the chamber and the opening of the chamber was covered with nylon gauze. To acclimate the spider to the chamber, the chamber was maintained at 15°, 20°, or 25° C for 1 h before the measurement. The cover was removed and the chamber was hermetically sealed with a silicone-rubber plug. An initial gas sample of 200 μ l was taken from the chamber with a gas-tight syringe. Oxygen concentration was determined by gas chromatography. The gas pressure inside the chamber was equilibrated with the surrounding pressure by piercing the plug with a fine hypodermic needle. The needle was removed and the chamber was incubated at 15°, 20°, or 25° C in darkness for 5 h (instar 1) or 3 h (the other instars), then a final gas sample was analyzed. All measurements were converted to STPD.

To measure the metabolic rate associated with web-spinning, larger respiratory chambers consisting of glass vials of 11.5 ml, or glass flasks of 35, 65, and 125 ml were used. The inside surfaces of these chambers were not covered with nylon gauze, to facilitate the removal of silk from the chamber (see below). The chamber was incubated at 15°, 20°, or 25° C in darkness for 24 h. Oxygen consumption was determined only in cases where spiders constructed a web in the chamber. After the measurement, the silk spun within the chamber was carefully collected by rolling it onto a glass rod and scraping off the silk fixed to the chamber wall using forceps and a small piece of silicone rubber attached to wire. Then the silk was dried at 80° C for 48 h and weighed using a Chyo M1-20A microbalance accurate to 1 μ g.

To estimate the average web weight in each instar of *A. limbata*, I determined the relationship between the area of sheet web and the total dry weight of web. The spiders of each instar were collected in the field of Nagoya University and released to a plastic container (33 × 17 × 24 cm) with a branch of *Eurya japonica*, on which *A. limbata* preferentially constructs the web in the field, or to a screen cage in which potted shrubs of *E. japonica* were placed. After 1 or 2 days, the area of sheet web was determined. Since the sheet web is approximately rhombus-shaped, the

lengths of two diagonals of the sheet (a , b) were measured and the sheet area was calculated as $(ab)/2$. The debris and dust were removed from the web and the silk was collected using a glass rod and forceps. The silk was dried at 80° C for 48 h and weighed.

Field survey

The population of *A. limbata* was surveyed for instar 3 to adult in the field of Nagoya University, to determine the rates of web relocation and mortality. The study area is a woody field covering 1680 m², which mainly consists of deciduous or evergreen broad-leaved trees (for details, see Tanaka in prep.). The spiders were individually marked with dots of model-aircraft paint on the tibia of leg-pairs 2, 3, and 4. The location of individual webs was identified by attaching a numbered tag to the vegetation supporting the web. If a marked spider disappeared from the original web site and was found at a new site, this was defined as web relocation, but if it was not found in the study area, then it was defined as mortality. The surveys were conducted 3–6 days a week from April to August 1982.

To obtain the average size of web for each instar, the area of sheet web was measured in this field. I carefully ran a wire, marked off at centimeter intervals, through the barrier web without destroying the web or disturbing the spider, and measured the diagonals of the sheet web.

Results

Standard metabolic rate

The relationship between body weight of spider (W , mg) and oxygen consumption rate (M , μ l/h) in non-active individuals was investigated at 15°, 20°, and 25° C (Fig. 1). The regressions are presented as the base-10 log-transformed formula:

$$\log M = \log a + b \cdot \log W.$$

Since log transformation introduces a systematic bias into the calculations (i.e. underestimate of M), a correction factor (CF) is necessary to counteract the bias (Baskerville 1972; Sprugel 1983). The correction is made as follows:

$$M = CF \cdot a \cdot W^b,$$

$$CF = \exp(SEE^2/2),$$

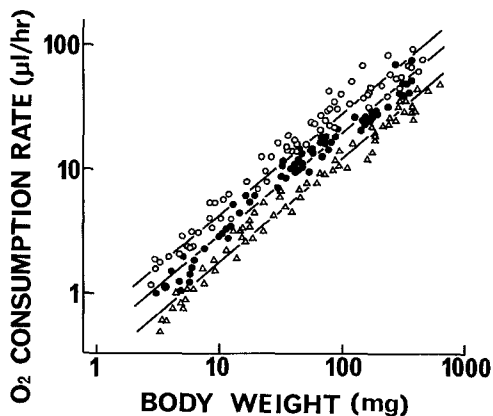


Fig. 1. Relationships between body weight and standard metabolic rate in *Agelena limbata*. Δ 15° C, \bullet 20° C, \circ 25° C

Table 1. Coefficient of regression of standard metabolic rate (M , cal) on temperature (T , °C) ($\log M = a + bT$), average body weight, average temperature in the field, and daily standard metabolic rate (DSMR) in *Agelena limbata*

Stage	a	b ($\times 10^{-2}$)	Body weight (mg)	Temperature (°C)	DSMR (cal)
Instar 1	-1.585	3.94	4.1	14.7	0.10
Instar 2	-1.272	3.86	9.4	16.4	0.23
Instar 3	-0.980	3.82	20.8	18.1	0.52
Instar 4	-0.716	3.76	42.1	20.4	1.13
Instar 5	-0.415	3.72	95.9	21.4	2.41
Instar 6	-0.144	3.66	197.5	21.0	4.21
Adult	0.133	3.60	415.1	23.5	9.53

Table 2. Metabolic increment in web-spinning activity (A values, cal/mg) of *Agelena limbata*

Stage	15° C	20° C	25° C
Instar 1	1.24 ± 0.76 (10) ^a	1.18 ± 0.60 (8)	1.89 ± 1.29 (13)
Instar 2	1.72 ± 0.62 (8)	1.47 ± 0.80 (10)	1.92 ± 1.59 (8)
Instar 3	1.29 ± 0.60 (11)	2.11 ± 0.77 (10)	2.70 ± 1.50 (10)
Instar 4	1.92 ± 1.39 (10)	2.39 ± 1.26 (11)	2.42 ± 1.89 (11)
Instar 5	1.99 ± 0.69 (10)	2.14 ± 0.87 (10)	1.80 ± 0.79 (10)
Instar 6	2.11 ± 0.58 (10)	2.22 ± 1.04 (9)	2.16 ± 0.79 (10)
Adult	1.79 ± 1.96 (10)	2.39 ± 1.03 (9)	2.31 ± 0.96 (10)

^a Mean ± SD. The figures in parentheses indicate sample sizes

where SEE is the standard error of estimate of the regression in the natural (base e) log-transformed formula and is calculated from a base-10 SEE by multiplying by $\log_e 10$ (= 2.303). All allometric equations in this paper were obtained in this manner.

The regression equations presented in Fig. 1 are:

$$15^\circ \text{C: } M = 0.268 W^{0.830} \quad (r^2 = 0.924, N = 65), \quad (1)$$

$$20^\circ \text{C: } M = 0.445 W^{0.823} \quad (r^2 = 0.966, N = 67), \quad (2)$$

$$25^\circ \text{C: } M = 0.679 W^{0.814} \quad (r^2 = 0.949, N = 68). \quad (3)$$

The daily standard metabolic rates (DSMR) were calculated from the average body weight of spiders and the average field temperature (Tanaka unpublished), using Eqs. (1)–(3) and the regression of metabolic rate on temperature (T , °C) of $\log M = a + b \cdot T$ (Table 1). These values were converted to calorific values, assuming an oxy-calorific coefficient of 0.00483 cal/ $\mu\text{l O}_2$ (Table 1).

Energetic cost of web construction

The metabolic increment for web-spinning activity was obtained by subtracting the standard metabolic rate, as estimated from the body weight of the individuals using Eqs. (1)–(3), from the overall metabolic rate observed during web-spinning within the respiratory chamber. The obtained value (oxygen consumption rate) was converted to calorific value and expressed as cal per unit weight (mg) of silk spun in the chamber (A values, Table 2). Relatively smaller A values were observed at 15° or 20° C than at higher temperatures, but the differences were not significant among temperatures except for instar 3 ($P > 0.05$, Kruskal-Wallis test). There were also no significant differences among instars ($P > 0.05$). I assumed, therefore, a constant A value of 1.99 cal/mg, the mean of all data, regardless of temperature or instar.

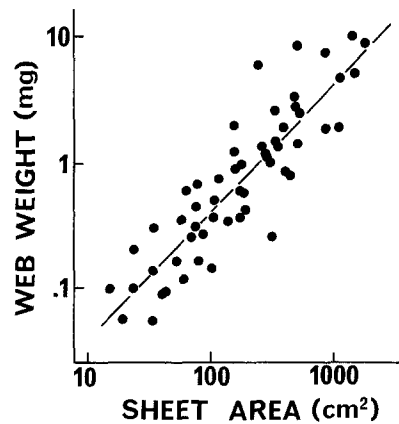


Fig. 2. Relationship between area of sheet web and dry weight of whole web in *Agelena limbata*

Table 3. Area of sheet web, weight of web, energy cost of web construction (C_w) and ratio of C_w to daily standard metabolic rate (C_w/DSMR) in *Agelena limbata*

Stage	Area of sheet (cm ²)	Web wt. (mg)	C_w (cal)	C_w/DSMR
Instar 1	41 ± 18 (25) ^a	0.20	1.3	13.2
Instar 2	108 ± 49 (40)	0.54	3.5	15.1
Instar 3	228 ± 92 (57)	1.15	7.4	14.4
Instar 4	647 ± 316 (88)	3.30	21.3	19.0
Instar 5	1066 ± 477 (66)	5.46	35.3	14.7
Instar 6	1865 ± 955 (43)	9.63	62.2	14.8
Adult	2522 ± 883 (27)	13.07	84.4	8.9

^a Mean ± SD. The figures in parentheses indicate sample sizes

I did not measure the calorific equivalent of silk (S , cal/mg). There are reports of S values in four species of spiders belonging to three families: 4.53 for *Nephila clavipes*, 4.56 for *Cyrtophora moluccensis* (Lubin 1973); 4.17 for *Leptyphantus zimmermanni* (Ford 1977); and 4.63 for *Sosippus janus* (Prestwich 1977). Only small differences are noted even though the webs of these species differ greatly in design, size, and adhesiveness. A constant S value regardless of species or web type is consistent with the fact that spider silk is a fibroin-type protein (Foelix 1982, p 109). Thus, I used a constant S value of 4.47, the mean of these four data.

Figure 2 shows the relationship between the area of sheet web (X , cm²) and the dry weight of whole web (W_w , mg) for the webs which were built in plastic containers or screen cage. The regression equation is:

$$W_w = (4.699 \times 10^{-3}) X^{1.013} \quad (r^2 = 0.759, N = 56).$$

The average area of sheet web for each instar was obtained in the field and the average weight of web (W_w) was calculated using this equation (Table 3). The energy costs of web construction (C_w) were estimated from W_w using the following equation (Table 3):

$$C_w = (A + S)W_w = 6.46 W_w.$$

The later instar spiders produced larger webs and thus expended more energy to construct a web. The C_w per se, however, is not always a good index of web-construction cost because the body size of spiders varies between instars or species. Standardization of cost is necessary to compare

Table 4. Daily rates of web relocation and mortality in *Agelena limbata*

Stage	Initial no. of spiders observed	Daily rate of web relocation (%)	Daily rate of mortality (%)
Instar 3	183	0.70 (17) ^a	3.98
Instar 4	131	0.30 (7)	2.61
Instar 5	107	0.44 (9)	1.98
Instar 6	109	0.14 (3)	1.65
Adult	47	0.0 (0)	2.27

^a The figures in parentheses indicate the numbers of individuals which relocated the web within the stage

the costs between instars or species. I standardized the web-construction cost by the daily standard metabolic rate (DSMR), i.e. a ratio of $C_w/DSMR$ (Table 3). The values of $C_w/DSMR$ in *A. limbata* were of similar orders of magnitude among instars though a relatively larger ratio was found in instar 5 and a smaller ratio in adults. Thus *A. limbata* individuals consume about 9–19 times the energy of daily maintenance cost to construct a web, suggesting an energetically costly web.

Rates of web relocation and mortality

Web relocation and mortality were investigated in spiders of instar 3 to adult (Table 4). Most of the relocators (30 of 36) built new webs at new sites. Some spiders, however, intruded into conspecific webs and occupied them. I observed (a) takeover of web ($N=2$); instar 3 spiders expelled instar 2 and 3 spiders, respectively, (b) reuse of abandoned web in instar 4 and 5 ($N=2$) and (c) exchange of webs by two individuals of instar 5 ($N=2$). In case (c), I suspected that an individual S1 intruded into the web W2 and expelled the owner S2, and so S2 searched for another web site and intruded into the web W1 which S1 had originally occupied and abandoned.

The rate of web relocation was low in every stage of *A. limbata* observed, below 1% daily (Table 4). Less than 10% of individuals observed at the beginning of a stage relocated webs during the stage. All relocators moved the web sites only once within the stage. These results show that *A. limbata* has high web-site tenacity. The daily rate of mortality was 1.65%–3.98%, higher than the relocation rate.

Out of a total of 36 relocations, 18 occurred within trees (intra-tree relocation) and the others were inter-tree relocations. The relocation distance, defined as distance between funnels of the original and new webs, was short (<1 m) in intra-tree relocations. The distance of inter-tree relocation was not long either; the maximum distance observed was 4 m and the mean distance was 1.4 ± 1.1 (SD) m ($N=18$). These results support the assumption that the major energetic cost of web relocation is that of energy to construct a new web.

Discussion

Energetic cost of web construction

This study is the first to evaluate the energetic cost of web construction of the spider in all stages. The energetic cost of web construction can be estimated by measuring three basic parameters, i.e. the net metabolic increment in web-spinning activity (A), the calorific equivalent of silk (S), and the web weight (W_w). Values of A do not differ significantly among instars or temperatures in *A. limbata*. Ford (1977) also reports constant A at different temperatures. Values of A vary, however, from species to species (Table 5). The metabolic energy expended in web-spinning activity presumably depends on the total length of silk thread spun, i.e. the distance of locomotion, rather than the total weight of silk. The value of A may, therefore, depend on the thickness of thread in relation to body size, because this value is silk-weight specific. Thus spiders which spin thicker threads relative to body size may have smaller A values. Further investigations are required on the thickness of silk thread or the weight of thread per unit length. On the other hand, values of S are similar among species (Table 5).

I evaluated and compared the cost of web construction among species or web types by the ratio $C_w/DSMR$ (Table 5). There are notable differences in $C_w/DSMR$ among species. The sheet-funnel web of *A. limbata* is characterized by a tight mesh of silk threads. The construction of this web requires much silk and much energy, 8.9–19.0 times the daily maintenance energy. The lycosid *Sosippus janus* makes a web, unlike other lycosids that are usually wandering spiders. The web of *S. janus* has a structure similar to the sheet-funnel web of agelenids, and therefore is energetically costly.

Table 5. Metabolic increment in web-spinning activity (A , cal/mg), calorific equivalent of silk (S , cal/mg), web weight (W_w , mg) and ratio of energy cost of web construction to daily standard metabolic rate ($C_w/DSMR$)

Species	Web type	Temperature (°C)	A	S	W_w	$C_w/DSMR$	Author
<i>Agelena limbata</i>	sheet-funnel	^a	1.99	–	^b	8.9–19.0	This study
<i>Sosippus janus</i>	sheet-funnel	25	1.00	4.63	20	23.6	Prestwich (1977)
<i>Leptyphantes zimmermanni</i>	sheet	{ 4.8 10 14.6	{ 2.57 2.49 2.77	4.17	0.0664	{ 8.2 5.3 4.0	Ford (1977)
<i>Araneus diadematus</i>	orb	25	0.80	–	0.1 ^c	0.021	Peakall and Witt (1976)
<i>Nephila clavipes</i>	orb	–	–	4.53	–	–	Lubin (1973)
<i>Cyrtophora moluccensis</i>	orb	–	–	4.56	–	–	Lubin (1973)

^{a, b} See Table 3

^c hypothetical value (see text)

Table 6. Daily rate of web relocation in spiders

Species	Web type	Daily rate of web relocation (%)	Author
<i>Agelena limbata</i>	sheet-funnel	0.0–0.70	This study
2 species	sheet	20–21 ^{a, b}	Janetos (1982)
12 species	orb	42–45 ^{a, b}	Janetos (1982)
<i>Argiope aurantia</i>	orb	18	Enders (1975)
<i>A. trifasciata</i>	orb	10	Enders (1975)
<i>Uloborus diversus</i>	orb	13 ^{a, c}	Eberhard (1971)

^a The data include the daily rates of web relocation and mortality.

^b The relocation rate (*RR*) was calculated from the residence time (*RT*) that Janetos presented, assuming the following equation: $RR = 1/RT$.

^c Eberhard reported the daily rate of web desertion of 17%. This figure included the individuals that built a new web at the same site several days later (24%). Then the daily rate of web relocation is calculated to be 13% (0.17×0.76)

Peakall and Witt (1976) estimated the web cost in the orbweaver *Araneus diadematus* by assuming the web weight to be 0.1 mg, though they did not actually measure the web weight. The orbweb of *A. diadematus* has a much lower cost than other types of web, e.g. about 1/1000 of the cost of *S. janus* web in terms of energy cost relative to daily maintenance. I believe that the web weight of 0.1 mg which they assume is an underestimate. However, even if the true weight is 10 times their estimate, the web of *A. diadematus* is still less costly than other webs. There are two possible reasons for the low cost of the *A. diadematus* web. First, orbwebs consist of a relatively sparse mesh of silk threads compared with other webs, hence require less silk. The second reason concerns silk-recycling behavior. *A. diadematus* ingests its old web and reuses the material for a new web. This recycling process is 92%–98% efficient (Peakall 1971). Some orbweavers have this trait, but others do not recycle the silk. There must be a great difference in web cost between these two types of orbweavers.

The cost of sheetweb of the linyphiid *Leptyphantus zimmermanni* falls between those of orbwebs and sheet-funnel webs (Table 5). This result is consistent with the design of its web, which consists of a mesh of silk strands coarser than that of sheet-funnel webs but finer than that of orbwebs. I conclude that the great differences in web-construction cost between species or web types may be due to total web weight, which is associated with mesh size and web size, and to whether each species recycles silk, rather than the weight-specific costs shown by *A* and *S* values.

Web relocation

I compared the rate of web relocation in relation to web cost among different types of web builders (Table 6). The sheet-funnel weavers which produce the most costly webs show much higher web-site tenacity than the orbweavers, which make the least costly webs. Janetos (1982) compared residence times at web sites between sheetweavers (Linyphiidae) and orbweavers (Araneidae, Tetragnathidae, Uloboridae). He estimated the web cost of sheetweavers based on data from the sheet-funnel weaver *Sosippus janus* presented by Prestwich (1977), confusing the sheet-funnel web, the most costly web, with the sheet web, a web of intermediate cost (see Table 5). However, his assumption that sheet webs

are more costly than orbwebs is not thereby falsified. He showed that the sheetweavers relocated web sites less frequently than the orbweavers (Table 6). The data of Janetos (1982) and Eberhard (1971) combine mortality and web relocation, while the present study and that of Enders (1975) discriminate between the two. However, the daily rate of disappearance, which includes both mortality and web relocation, is still low, 1.79%–4.68%, in *A. limbata* (see Table 4). I conclude that the energy cost of web construction is important in determining the frequency of web relocation. However, there are various types of webs other than those listed in Tables 5 and 6 which vary in terms of energy for construction. Further studies on web relocation are needed in many types of web builders to test the hypothesis that spiders which construct more costly webs will relocate webs less frequently.

Factors other than cost of web construction may affect web relocation, e.g. prey availability (Turnbull 1964; Olive 1982), kleptoparasitic load (Rypstra 1981), web damage by wind (Eberhard 1971), and territorial disputes with conspecifics (Riechert 1982). Prey availability also affects the decision as to web relocation in *A. limbata*, where a low rate of prey capture induces the spider to leave a web site (Tanaka in prep.). The low frequency of web relocation of *A. limbata* observed in the field, however, may not be due to high rate of prey capture because food limitation is suggested in *A. limbata* (Tanaka in prep.). Web relocation should be monitored under controlled food conditions.

Why does *A. limbata* construct a costly web?

This paper reveals that *A. limbata* has high web-site tenacity probably because construction of new webs is costly. Since spiders search for good web sites by web relocation (Turnbull 1964; Olive 1982), and the high cost of web construction limits web relocation, then the spider may not be able to respond well to variation in profitability of web sites. Why does *A. limbata* produce such a costly web in spite of disadvantages of cost per se and behavioral limitation? The high cost of this spider's web is certainly due to its design, i.e. the tight mesh of silk threads, which needs much silk. One element of web design is the adhesiveness of the silk line. High adhesiveness may reduce the amount of silk in web by enhancing its effectiveness in prey capture. The adhesive orbwebs consist of a sparse mesh of silk lines and have low construction costs. By contrast, non-adhesive webs have a fine mesh and three-dimensional structure to prevent prey from escaping through silk lines, which in turn requires much silk. The sheet-funnel web of *A. limbata* has an extremely small mesh-size and looks like cloth. I have sometimes observed that prey insects pursued by *A. limbata* could escape through a small hole that had been made in the sheet web by some object. The web of *A. limbata* may need a fine-mesh structure in order to function effectively as trap.

Non-adhesive webs do have some advantages. If dust attaches to an adhesive web and reduces its adhesiveness, the spider has to reconstruct the web. On the other hand, spiders with non-adhesive webs need not reconstruct the web if the web is not damaged or destroyed. Furthermore, a fine-mesh web is tough and is not destroyed easily. If the spider keeps the web at the same site, a non-adhesive web will cost less for maintenance. Hence, spiders that build non-adhesive webs with high construction costs may tend

to stay at the same web site even though food conditions are poor. The adult spiders can survive starvation stresses for a long time (Anderson 1974; Tanaka and Itô 1982; Tanaka et al. 1985). In *A. limbata*, even instar-1 nymphs can survive more than 20 days of starvation (Tanaka in prep.). This trait enables *A. limbata* to be tenacious on the same web site even under poor food conditions.

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