# THE ENERGY BUDGET OF AN ORB WEB-BUILDING SPIDER

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Abstract—1. First measurements of increased total oxygen consumption of web-building *Araneus diade*matus spiders over resting animals are reported for nine webs of an adult female.

2. Analysis of movie pictures and web photographs results in an estimate of the number of steps and the amount of up and down movement which the animal used in construction of a single web. 3. Combination of both measures permits calculation of step energy, which can be added to the chemical energy involved in silk recycling, to lead to an appraisal of advantages and disadvantages involved in the daily construction of individual orb webs by single animals.

4. This is compared to data from the literature on the web-building strategies of other spiders.

### INTRODUCTION

ORB-WEB building spiders have developed a highly specialized strategy for survival: Long periods of immobility alternate with a relatively short burst of activity, when a web is constructed or a fly caught and wrapped in the web. All this is made possible through maximum use of silk: everywhere the animal moves it lays a silken thread, it catches the prey in a silken web and then wraps it in a silken bag. Each web is built and used by one animal alone.

One way of assessing the relative advantages of single trap building is to calculate the energy cost of the spider's activities. Silk has to be produced, its quantity and turnover can be measured and the resulting figures can be added to those expended in movements used to lay down the silken thread. Webmeasurements on photographs have been found to be such a convenient and accurate record of the builder's movements, that they have been extensively used to gauge changes in behaviour caused by stress factors in the environment (Witt, et al., 1968; Witt, 1971a). In this paper we evaluate the photographic record of the Araneus diadematus (Clerck) web together with movies of web construction to determine the number of steps which were necessary for trap construction. A combination of oxygen consumption measurements in spiders with movement data permits us to assess the daily energy costs of a web-building spider's activity.

Our data can be compared to those obtained by other authors (i.e. Edgar, 1971) for wolf spiders like *Pardosa lugubris*. These animals hunt prey in direct attack, and use silk only very sparingly. They find their prey on the ground, where size abundance and movement are necessarily quite different from the lofty heights, where *Araneus* constructs its trap. And though Edgar states that his wolf spiders in the field spend much of their time motionless, it can be assumed that they move more in 24 hr than the web builder with its 30–60 min daily building activity plus altogether only a few more minutes spent in running to the entangled prey and wrapping it.

Another strategy for prey-catching is used by those spiders which build small orb webs plus extensive "barrier webs". The latter supposedly knock-down prey, which then gets entangled in the trap of the orb (Kullmann, 1958; Lubin, 1973). Here silk renewal appears much less frequent (it takes an adult spider 3 days to construct a web) and some structures are used by several animals together, rather than by a single *Araneus diadematus*. This may be a compromise between the hunting and the orb-trapping methods; it requires a different distribution of expenditure between step-energy and silk-renewal-energy.

Without trying to provide a total figure for the ecological energetics of the web-builder, we have in this study undertaken to report on actual measurements of the energy cost of web-building. Thereby figures become available to other investigators which together with observations of life-span, growth, webefficiency, prey abundance and many others can serve as the basis for an assessment of the advantages and restrictions which orb-web construction presents in comparison to other prey-catching strategies.

#### **METHODS**

All studies were carried out on the cross spider, *Araneus diadematus* Clerck. Details on raising and maintaining this species in the laboratory have been described previously (Witt, 1971b).

Calculations of the number of steps involved in web construction were made in a frame-by-frame analysis of movie films. The sequence of events in the construction of an orb-web have been carefully observed and described, for instance by Savory (1952). Only the briefest summary can be given here: The web is constructed within a framework which in nature may be threads attached to the branches of a bush and in the laboratory a silken thread runs around the edges of the box to form a framework (see Fig. 1). This earliest phase is difficult to record on film,

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Fig. 1. On this photograph of the web of an adult female *Araneus diadematus* Cl. spider, parts of the structure have been marked; frame, radii and spiral lengths are used—in addition to movie pictures—to count the number of steps employed in construction. Note the relatively large sections of spiral between neighboring radii in the periphery, which we counted as 3 steps, as compared to one-step distances toward the hub. Table shows that in measuring spiral steps we discriminated between full and partial (pendulum) spiral turns.

as web-building is readily inhibited by the observer's activities at this stage (see Salzmann & Witt, 1973). The number of steps involved initially are estimated from the length of the frame thread. Then the radii are laid down and number of steps involved is counted for each radius. A provisional spiral is then laid from the center out and finally the sticky spiral laid down from the outside in. Frame-by-frame observations allows one to count the number of steps for each section of the spiral as it stretches from one radius to the next. This number of steps decreases as the center is approached (Jacobi-Kleemann, 1953). One step can be roughly defined as one forward plus backward movement of a front leg (see Fig. 2). In this way the total number of steps involved in web-building can be arrived at with reasonable accuracy.

The films were not made concurrently with the oxygen measurements, but were made earlier on the same species maintained in cages of the same dimensions. The size, age and weight of the individuals for the two sets of experiments were closely matched. The potential energy involved in web-building was calculated from still photographs and the known weight of the spider at the time of web construction. The technique of photography of the web has been described previously (Witt, 1971b).

Oxygen consumption was measured by a differential micro-Warburg apparatus connected to two identical airtight transparent plexiglas cages. In some experiments an empty cage was used as a control to that containing the spider. In other experiments a non-web-building spider was used as a control to one active in web-building. Both cages were placed in a wooden box with plastic windows and lid and the Warburg apparatus mounted on the lid. The entire apparatus was maintained in an air-conditioned room at 25°C. Carbon dioxide was absorbed with soda–lime in a tray at the bottom of the cages.

## RESULTS

The number of steps involved in the formation of a single orb-web are detailed in Table 1. Gold (1973), re-examining the data of Schmidt-Nielsen (1972), found that the same energy was expended by all animals to carry a unit of their body mass one "step". For running, this figure is  $3 \times 10^{-4}$  cal g<sup>-1</sup>/step. Using this figure, the energy cost of steps involved in web-building can be calculated. The vertical distance traveled for each radius and spiral turn can be measured for each web from still photographs. The total work involved in potential energy, in g cm, can



Fig. 2. The spider moves from left to right, laying down spiral turns as she crosses from one radius to the next. The cephalothorax of the animal points to the right, the left front and hind legs to the hub of the web. Note that in A the two front legs are on radius 2 and in B the same legs touch radius 3, having gone one step. The four middle legs may perform several forward and turning movements during the same period of time; but this is not considered in our calculation (for detail of movements compare Jacobi-Kleemann, 1953).

Table 1. Number of steps and potential energy cost of formation of orb-web (Fig. 1). Weight of spider 115.4 mg

adius No.	No. of Steps	Vert. Distance cm.	Spiral No.	Vert. Distance cm.
1	22	22.0	1	8.8
2	21	17.2	2	10.0
3	20	15.3	.3	11.0
4	18 •	14.0	4	12.0
5	17	7.5	5	12.9
6	15	5.0	6	13.8
7	17	1.7	7	14.8
8	19	4.5	8	15.8
9	20	8.3	9	16.7
10	21	9.7	10	18.0
11	22	12.8	11	18.7
12	21	11.0	12	19.9
13	19	9.2	13	21.0
14	17	7.2	14	22.8
15	15	5.0	15	1.8
16	15	0.3	16	2.3
17	17	2.5	17	2.8
18	19	7.0	18	3.2
19	19	9.7	19	3.8
20	20	14.2	20	5.0
21	21	16.5		
22	22	19.7		
Total	417	220.3		235.1

Steps involved in spiral turns. Spiral 10-14 3 steps/radius 3x22x5 = 330 5-9 2 steps/radius 2x22x5 = 220 1-4 1 steps/radius 2x22x5 = 120Pendulum turns 3 steps/radius 3x7x5 = 105Provisional spiral 7 turns 0 3 str 3x7x2 = 462Steps for initial frame, considered one complete trip around the cage, number of steps estimated from observations on non-web building spider = 240 steps. Potential energy cost 2 x cage height = 1000 g mcs Total steps 417 + 1227 + 240 = 1884Potential energy (220 + 235 + 100) x 0.115 = 651 x 10<sup>-4</sup> cal. P.e.  $63.8 \times 2.34 \times 10^{-4} x$  0.115 =  $650 \times 10^{-4}$  cal.

then be calculated as the weight of the spider is known. These values are also detailed in Table 1.

Oxygen consumption was measured under three conditions. The first represents the basal metabolism of the spider when it was not involved with webbuilding, i.e. no webs were built for 2 days before or after the measurements were made. The second is for the basal metabolism of the spider at a time that it was building a web daily, but not during actual formation. Third, during the actual period of web formation. No difference was found in the basal metabolism between web-building and non-web-building individuals (Table 2). During web formation itself the levels of oxygen consumption were increased by approx 50% (Table 2).

#### DISCUSSION

The value for the basal metabolism of Araneus diadematus at 25°C is 360  $\mu$ l/g per hr (Table 2). This value is within the range found by Anderson (1970) for a variety of Arachnids, although it is close to the upper limit. Anderson did not make measurements on the genus Araneus, and his measurements were made at 20°C. For Lycosid spiders, Moulder & Reichle (1972) give values of 150  $\mu$ l/g per hr at 15°, 260  $\mu$ l/g per hr at 20° and 307  $\mu$ l/g per hr at 25°C. These figures show that oxygen consumption data markedly depend on temperature. Lubin (1973) gives values for Nephila which calculate out at 320  $\mu$ l/g per hr at 30°C. While no previous data appear to be available for Araneus, the values obtained here for the basal metabolism are in line with those obtained by previous workers on other species of *Arachnids*.

The use of the oxygen consumption technique does not appear to have been used previously in the calculation of the energy involved in web formation. Subtracting the basal metabolism, the oxygen consumption involved in the additional work of webbuilding is 144  $\mu$ l O<sub>2</sub>/g per hr using a conversion factor of 1  $\mu$ l = 0.0048 (Englemann, 1961) and a body weight of 115 mg, this is equivalent to 795 × 10<sup>-4</sup> cals, which is very close to the value calculated by step-energy (Table 1). This agreement gives experimental validity to the step energy approach for calculations of the cost of various activities of spiders.

In addition to web-building, an additional cost to the spider is the formation of the silk protein itself. Lubin (1973) calculated the energy content of webs by direct bomb calorimetry. Unfortunately the values obtained in this way have no biological meaning. This technique gives the energy required to synthesize silk from carbon dioxide, water and nitrogen oxides. In practice the spider starts from aminoacids and further uses a very effective re-cycling device. Araneus diadematus eats its own web daily and re-uses the material for the next web (Breed et al., 1964). This process has been shown to be 92-96% effective (Peakall, 1971). The breakdown of macromolecules to smaller structures releases energy, while energy must be supplied in the reverse process. In theory there is no net energy change. Morowitz (1968) calculated that 3.8% of the biomass is oxidized in each cycle. This figure is in good agreement with previous experiments in re-cycling (Peakall, 1971). Lubin (1973) gives a value of 4550 cal/g for the energy needed to recycle the web; and if the weight of a web of Araneus diadematus is 0.1 mg, the energy cost of silk formation becomes:

$$4550 \times 4 \times 10^{-2} \times 0.1 \times 10^{-3}$$
  
= 182 × 10^{-4} cals

The above figures can be used as a basis for the calculation of the energy involved in various strategies of prey-catching, web replacement and repair. Spiders confined in cages lead lives rather similar to those in the wild as far as web building is concerned. Studies of color-marked individual *diadematus* show that webs are built in the same place day after day (Peakall, 1971). Thus measurements of the energy budget in the laboratory should be close to the energy budget of the spider in the natural environment. Additional information is required on the frequency and calorific content of prey. The spiders used, in the current study, some  $800 \times 10^{-4}$  cals in web-building and

 
 Table 2. Oxygen consumption of Araneus diadematus under various conditions

	µ10 <sub>2</sub> /g/hr <sup>*</sup> ± s.d.	Body weight mg ± s.d.	Sample size
Basal rate, spider active in web-building	360 ± 27	101 ± 14	10
Basal rate, spider not active in web-building**	339 ± 34	103 ± 12	9
Rate during actual web-building	504 ± 32	99 ± 13	9

corrected to 0°C and 760 mm Hg pressure.

"defined as no web for two days before and after measurements.

an additional  $200 \times 10^{-4}$  cals in silk formation. This is equivalent to about 3000 steps and can be considered as the capital investment in prey capture. Prey capture itself costs only about 50 steps. If only a single item is caught, then the cost is 3000 steps/item, whereas ten preys reduce this figure to 350 steps/item.

No attempt has been made to assess frequency of prey capture nor the calorific value of prey. Robinson & Robinson (1973) have stated that Nephila maculata renews its orb webs less frequently before egg laying, but the webs were still functional. This shows that under especially challenging conditions, Nephila webs are not renewed and can still be used for several days. The data for the amount of prey they counted in their webs in New-Guinea can hardly be transferred to our Araneus webs. Lubin (1973) finds the horizontal orbbarrier-web combination of Cyrtophora moluccensis of lower trapping efficiency than the vertical Nephila web and it would be worthwhile to compare their construction frequency, prey abundance and building energy with Araneus data, using similar calculations as ours.

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