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Energy Costs of the Predation Strategy of the Web-Spinning Spider *Lepthyphantes zimmermanni* Bertkau (Linyphiidae)

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Summary. The energy costs of the predation strategy of the web-spinning spider *Lepthyphantes zimmermanni* were investigated in the laboratory. The standard respiratory costs associated with the stationary aspect of the strategy were estimated by means of a Gilson respirometer run at the different temperatures prevailing month by month in the beech woodland litter layer which comprises the spider's natural habitat. Respiration rate is related to weight by an exponent with a mean value of 0.7398. The Q_{10} of respiration rate is 2.41 between 5° C and 10° C and 1.97 between 10° C and 15° C. The energy costs of producing a web comprise the active respiratory costs associated with the locomotory activity involved in spinning a web together with the energy value of the silk used in the web manufacture. The former were evaluated by allowing a spider to spin a web in a respirometer, subtracting the calculated standard respiratory energy costs for a spider of equivalent weight and multiplying by a correction factor for web size. The relationship between spider weight and area of web produced was established in the laboratory. The respiratory cost of spinning a web is effectively constant with temperature at $724.46 \cdot 10^{-3}$ J for an adult (4 mg) spider. The energy value of spider silk was estimated by means of a bomb calorimeter and found to be 17,435 J g^{-1}. The energy content of the silk of a single adult's web is 1.16 J, giving energy cost of web production of 1.88 J at all temperatures.

Introduction

Lepthyphantes zimmermanni Bertkau is a web-spinning linyphiid spider which, although common in grassy, and moorland areas over much of Britain (Duffey, 1974) is particularly abundant in woodland litter in the south where the spider spins a horizontally-orientated web at the litter/air interface. The web is rather

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irregular as its shape is determined by the availability of anchor-sites in the form of twigs and the petioles of dead leaves. Unlike that of argiopid spiders, linyphiid silk is not sticky and so the webs are not replaced regularly. Once a linyphiid has produced a web it will maintain its position unless the web is destroyed or if food availability is drastically reduced; even in the complete absence of food the spiders are very tenacious in maintaining their position (Ford, 1975).

A spider such as *L. zimmermanni* can be considered as a Type I or "sit-and-wait" predator in the nomenclature of Schoener (1969, 1971). Schoener characterized such predators as being animals which do not expend time and energy in searching for their prey. It is generally accepted that when Schoener refers to the time and energy costs of search he is referring to the costs associated with locomotory activity; but it could be argued that time an energy are expended in search by *L. zimmermanni* in that the spider constructs a web in order to search the environment. However this is a once-and-for-all expenditure and there is no individual cost associated with each prey item.

The energy costs of the predation strategy of *L. zimmermanni* comprise: a) the standard or maintenance respiratory costs associated with the sit-and-wait aspect of the strategy when the spider is waiting in its web; b) the active respiratory costs associated with the locomotory activity involved in spinning a web; c) the energy value of the silk used to manufacture the web: this being part of the spider's production.

These three costs were evaluated using *L. zimmermanni* adults obtained from a beech woodland litter layer in Brogden's Belt, Wytham Woods, Oxfordshire.

Methods

Temperature. A Grant thermistor temperature recorder was used to calculate mean monthly temperatures in the litter layer at Brogden's Belt. Of necessity, these temperatures were established for the year before the respirometry experiments.

Standard Respiration Rate. Oxygen consumption was measured over 24 h using a refrigerated GR14 model of the Gilson differential respirometer (Gilson, 1963) as described in Ford (1977). To eliminate acclimation effects, animals were run in the respirometer at the mean monthly litter temperature of the month in which they were collected. In practice this meant running the animals at the temperature established for the appropriate month of the previous year. At the end of the experiment the spiders were anaesthetized with carbon dioxide and weighed on an electromicrobalance.

Active Respiration Rate Associated with Spinning a Web. In order to measure the respiratory energy costs of web production, larger 15 ml respirometer flasks were used: these have a diameter of up to 4 cm and so provide sufficient room for the spinning of a small web. It was anticipated that if a number of spiders were placed in dry (to provide firm anchor points) 15 ml flasks, a proportion of them would produce webs. Time did not permit of these experiments being conducted at each of the mean monthly temperatures so a compromise solution was arrived at whereby the experiments were performed on spiders obtained from the field in November, May and July at the temperatures appropriate to these months, i.e. 4.8° C, 10° C, and 14.6° C (Table 1). This approach has advantages of convenience and time but does not sacrifice the realism gained by using temperatures appropriate to those being experienced in the wild.

As the respirometer flasks were submerged in a water bath, it was impossible to establish the start and finish of web construction and hence the duration of the associated metabolic activity. To overcome this, respirometry runs were performed for the usual 24 h and then the spider was weighed. The standard 24 h respiratory energy expenditure of a spider of that weight and at that temperature could be calculated from the previous experiments on standard respiration rate. The difference between this and the actual energy expenditure gives a measure of the respiratory energy costs of building a web. Owing to the constraints imposed by the size of the respirometer flasks, the web produced in the respirometer is smaller than that which a spider of equivalent size would produce in the wild, and the associated metabolic costs are reduced. In order to apply an appropriate correction factor, the size of the web produced in the respirometer flask was estimated in situ by means of a pair of calipers.

Web-Size. Twenty *L. zimmermanni* adults were obtained from Brogden's Belt and fed to satiation in the laboratory. They were then allowed to spin webs at room temperature in aquaria containing short cylinders of wire mesh (diameter 10 cm and height 10 cm with mesh size 1 cm^2) to provide a three-dimensional environment. Spiders usually spun a web in a short period and this was then dusted with *Lycopodium* powder to render it more visible. Measurements were taken of the web using a pair of dividers and a full-scale drawing of the web was then produced on graph paper. The squares on the graph paper could then be used to calculate the area of the web. The spider that had produced the web was anaesthetized with carbon dioxide and weighed.

Energy Value of the Silk in a Web. In order to determine the energy content of a typical *L. zimmermanni* web it is necessary to establish the energy value of the constituent silk and the quantity of silk per web. Webs were collected from experimental animals over a period of time and stored over silica gel in a desiccator. The silk was eventually dried in a vacuum oven at 60° C, compressed into a pellet, weighed and then burned in a Phillipson bomb calorimeter (Phillipson, 1964). Accurate weighing of individual webs was not possible, so a combined weight of several webs was established and then divided by the constituent number of webs. Adult spiders weighing 4.0 ± 0.5 mg were fed in the laboratory and then allowed to spin webs in cylinders of wire mesh (see above). Each individual web was completely removed from the mesh and two lots of ten such webs were collected and placed in a desiccator. The individual webs were consolidated together by lightly rolling between the fingers to produce two balls of silk which were dried in a vacuum oven at 60° C and then weighed.

Results

The mean monthly temperatures recorded for the litter layer in Brogden's Belt in the year prior to the respirometry experiments (1971) are shown in Table 1. The temperature recorder was maintained in position during the following year which confirmed that the first year's data were not atypical (Ford, 1977). It will be seen that the litter temperatures recorded for November and December were identical at 4.8° C and so the total number of experimental temperatures used was 11 rather than 12.

In the experiments on standard respiration rate, a mean hourly rate was calculated for each experimental animal for the 24 h run. At each temperature, individual respiration rate in $\mu l\ O_2\ h^{-1}$ was plotted against live weight of spider in mg and regression lines were calculated through the data points. The equations of these regressions are given in Table 2 together with their correlation coefficients. The gradients of the regression lines give the exponent 'b' in the relationship $y = ax^b$ where y = respiration rate and x = live weight. The value of b in these experiments varies from 0.6318 to 0.8222 and has a mean value of 0.7398. Thus at a given temperature, respiration rate per unit weight decreases at higher

Table 1. Mean monthly temperatures recorded in the litter layer

Month	Temperature (°C)	Month	Temperature (°C)
January	2.9	July	14.6
February	2.8	August	14.0
March	4.0	September	12.7
April	6.7	October	9.1
May	10.0	November	4.8
June	9.6	December	4.8

Table 2. Regression equations of respiration rate against live weight for *L. zimmermanni* at different temperatures

Temperature	Regression equation	Correlation coefficient
2.8° C	$\log y = 0.6804 \log x - 0.8130$	$(r = 0.8033)$
2.9° C	$\log y = 0.7117 \log x - 0.8447$	$(r = 0.6735)$
4.0° C	$\log y = 0.8141 \log x - 0.8640$	$(r = 0.8761)$
4.8° C	$\log y = 0.8222 \log x - 0.8042$	$(r = 0.8024)$
6.7° C	$\log y = 0.8150 \log x - 0.7537$	$(r = 0.9260)$
9.1° C	$\log y = 0.7102 \log x - 0.6161$	$(r = 0.7689)$
9.6° C	$\log y = 0.6698 \log x - 0.5641$	$(r = 0.8373)$
10.0° C	$\log y = 0.7770 \log x - 0.5627$	$(r = 0.8843)$
12.7° C	$\log y = 0.7701 \log x - 0.5072$	$(r = 0.7755)$
14.0° C	$\log y = 0.6318 \log x - 0.4044$	$(r = 0.8238)$
14.6° C	$\log y = 0.7356 \log x - 0.4488$	$(r = 0.8205)$

weights and in order to examine the effect of temperature upon respiration rate it is best to examine the data for a spider of one particular weight. In this study 4 mg was used as the weight of a standard *L. zimmermanni* as this was found empirically to be a typical weight for an adult of the species. Thus by substituting $x = 4$ in the equation given in Table 2, the relationship between temperature and standard respiration rate for a *L. zimmermanni* spider weighing 4 mg can be demonstrated, as in Figure 1. This relationship has the form:

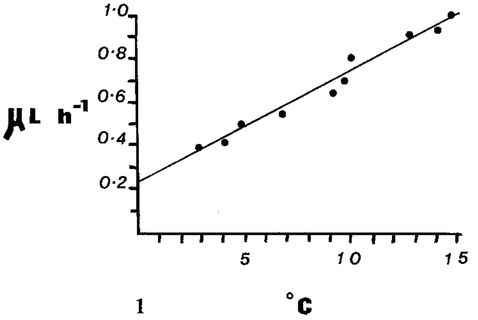
$$y = 0.0516\,x + 0.2279 \quad (r = 0.9909).$$

Similar graphs for other weights of spider can readily be produced by substituting other values of x in the equations in Table 2.

Figure 1 may be used to calculate the Q_{10} of the respiration rate of *L. zimmermanni* from the formula:

$$Q_{10} = \left(\frac{M_2}{M_1}\right)^{10/t_2 - t_1}$$

where M_1 = respiration rate at temperature t_1 and M_2 = respiration rate at tem-



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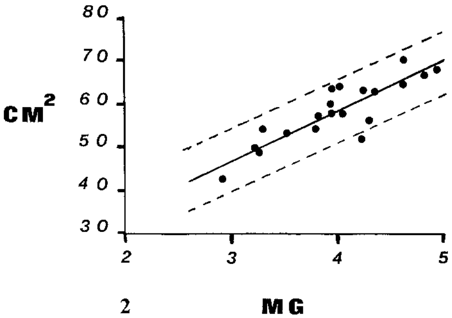

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Fig. 1. Relationship between temperature and standard respiration rate for a *L. zimmermanni* adult of weight 4 mg

Fig. 2. Relationship between spider weight and area of web produced. The dashed lines represent the 95% confidence limits

Table 3. Calculation of the respiratory energy cost of spinning a web at different temperatures in *L. zimmermanni*

Measured O_2 consumption 24 h^{-1}	Wt. of spider	Predicted O_2 consumption 24 h^{-1}	Excess of measured over predicted	
in µl O_2	in mg	in µl O_2	in µl O_2	in $J \cdot 10^{-3}$
4.8° C				
16.96	4.32	12.56	4.40	88.37
17.06	3.98	11.73	5.33	107.04
18.21	4.65	13.33	4.88	98.01
16.21	4.24	12.35	3.86	77.52
10.0° C				
20.71	3.82	18.61	3.10	62.26
22.58	3.73	18.27	4.31	86.56
26.42	4.35	20.59	5.83	117.09
24.78	4.28	20.33	4.45	89.37
25.10	4.41	20.81	4.29	86.16
21.64	3.69	18.12	3.52	70.69
14.6° C				
28.32	3.67	22.22	6.10	122.51
30.15	4.41	25.42	4.73	94.99
26.84	3.78	22.71	4.13	82.94
25.21	3.54	21.64	3.57	71.70
31.52	4.82	27.17	4.35	87.16
30.40	4.33	25.10	5.36	107.65

perature t_2. The value of Q_{10} between 5° C and 10° C is 2.41 and between 10° C and 15 ° C is 1.97.

Turning to the measurement of the active respiration rate associated with spinning a web, Table 3 shows the total amount of oxygen consumed over 24 h by *L. zimmermanni* individuals spinning webs in the respirometer. Also shown, for each animal, is the predicted 24 h consumption for a spider of that weight

Table 4. The respiratory energy cost of spinning a web in *L. zimmermanni*, expressed on a weight-specific basis

Wt. of spider in mg	Excess respiratory energy cost in $J \cdot 10^{-3}$	Wt.-specific excess respiratory energy cost in $J \cdot 10^{-3}\,mg^{-1}$
4.8° C		
4.32	88.37	20.46
3.98	107.04	26.89
4.65	98.01	21.08
4.24	77.52	18.28
10.0° C		
3.82	62.26	16.30
3.73	86.56	23.21
4.35	117.09	26.92
4.28	89.37	20.88
4.41	86.16	19.54
3.69	70.69	19.16
14.6° C		
3.67	122.51	33.38
4.41	94.99	21.54
3.78	82.94	21.94
3.54	71.70	20.25
4.82	87.16	18.08
4.33	107.65	24.86

from the appropriate standard respiration rate equation in Table 2. The difference between the two gives the metabolic cost of spinning the web which is shown in Table 3 in the original units of $\mu l\ O_2\ h^{-1}$ and also converted into energy units (Joules) by means of an oxygen-energy equivalent ($1\ \mu l\ O_2 = 20.0832 \cdot 10^{-3}$ J). The energy cost of web-spinning can not be expressed in the form of a rate as no information is available on the time taken to complete the web.

Owing to the constraints imposed by the volume of the respirometer flask and the space taken by the central well containing NaOH, all the webs produced were roughly circular with a measured diameter of 3 cm. This gives an estimated area of 7.07 cm^2 (πr^2, $r = 1.5$). Data concerning the size of web produced in unconstrained situations are shown in Figure 2 which indicates that there is a clear relationship between weight of spider and size of web produced in the laboratory, the relationship having the form:

$$y = 11.66\ x + 11.55$$

All the spiders used in this experiment had been fed to satiation and so the size of web produced should not have been limited by the amount of energy available for silk production.

From Figure 2 it can be deduced that a *L. zimmermanni* spider weighing 4 mg (a standard adult weight—see above) will produce a web with an area of 58.19 cm^2 if unconstrained, whilst all spiders produced a web with an area of approximately 7.07 cm^2 in the respirometer. Thus a correction factor for

Table 5. The respiratory energy cost to an adult (4 mg) *L. zimmermanni* of spinning a typical web at different temperatures

Temperature	Mean wt.-specific energy cost in $J \cdot 10^{-3}$ mg^{-1} (see Table 4)	Total energy cost for a 4 mg adult producing a web of area 58.19 cm^2 ($J \cdot 10^{-3}$)
4.8° C	21.68	713.71
10.0° C	21.00	691.32
14.6° C	23.34	768.35

web size must be applied to the data in order to obtain a figure for the metabolic cost of producing a typical web. This factor is 58.19/7.07 which is 8.23. A correction for the weight of the spider is also necessary: although only adults were used to obtain the data in Table 3, there is still considerable individual variation in weight and this will clearly have an effect on the measured metabolic rate. To overcome this, the excess respiratory cost associated with spinning a web is expressed on a weight-specific basis as in Table 4. The mean value obtained for each temperature can then be multipled by 4 to give the respiratory energy cost to a 4 mg animal of spinning a web of the size found in a respiratory flask and then by the correction factor 8.23 to give the best estimate of the respiratory energy cost of spinning a typical web in the wild for a standard 4 mg animal. This is done in Table 5 where it can be seen that the values at the three different temperatures are very similar, the mean being $724.46 \cdot 10^{-3}$ J.

Having established the respiratory energy cost of web production, it only remains to establish the energy value of the silk used in spinning the web. Determination of the ash-free energy equivalent of the silk of *L. zimmermanni* by means of the Phillipson bomb calorimeter yielded a figure of 4 167 cals g^{-1}. The energy content was determined in terms of calories rather than Joules as the initial calibration of the bomb calorimeter was in terms of the former units. Conversion to Joules entails multiplication by 4.184, giving a value of 17 434·73 J g^{-1}. The dry weights of the two balls of silk consisting of ten *L. zimmermanni* webs each were 0.5918 mg and 0.7362 mg, giving a mean value of 0.6640 mg. The mean dry weight of silk per web is thus 0.0664 mg which in energy terms is equivalent to 1.1577 J.

Discussion

The standard respiration rate measured in this study represents the basic energy cost of the sit-and-wait predation strategy of *L. zimmermanni*. As the exponent relating weight to respiration rate has a mean value of 0.7398, it can be seen that this relationship is indirect and so a standard weight of 4 mg was used to bring out the relationship between temperature and respiration rate of an adult *L. zimmermanni*, as shown in Figure 1. In order to express this relationship in energy terms it is necessary to multiply the data by the oxycalorific conversion

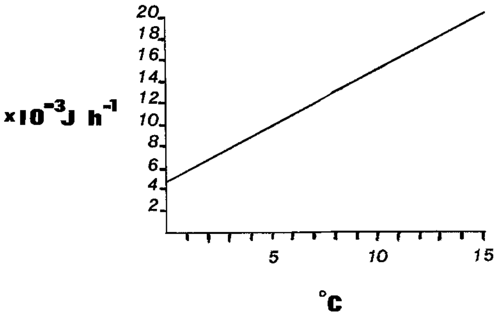

Fig. 3. Relationship between temperature and respiratory energy costs for an adult *L. zimmermanni* of weight 4 mg

factor of $20.0832 \cdot 10^{-3}$ J μl^{-1} O_2 as has been done in Figure 3 where it is shown that the relationship has the form:

$$y = 1.0363\ x + 4.5769$$

where x = temperature in °C and y = respiratory energy costs in $J \times 10^{-3}\ h^{-1}$. This relationship can be used to establish the total daily respiratory energy costs of maintenance metabolism at the three temperatures used in the experiments on the respiratory energy costs of web construction. These maintenance costs vary from $229.23 \cdot 10^{-3}$ J at 4.8° C through $358.56 \cdot 10^{-3}$ J at 10° C to $472.97 \cdot 10^{-3}$ J at 14.6° C. As can be seen from Table 5, however, the energy cost of producing a web is approximately constant at these three temperatures with a mean value of $724.46 \cdot 10^{-3}$ J. The reason why this energy cost is the same at different temperatures is presumably because, although the associated metabolic rate will be lower at low temperatures, the rate of movement of the spider will be slower and so the time taken to spin a web will be lengthened. The interaction of these two factors will produce an approximately constant energy cost with the construction of the web. Clearly although the absolute value is constant, when considered in relation to the animal's daily maintenance costs, its significance is greatest at lower temperatures.

There appear to be no figures in the literature with which to compare the value obtained in this study for the amount of energy present in the silk of a spider's web. The fact that silk is a protein suggests that its calorific value should be low: Petrusewicz and Macfadyen (1970) and Macfadyen (1963) give a figure of 4150 cal g^{-1} for plant protein and 3900 cal g^{-1} for animal protein, though without any indication of the range of values for either figure. The value of 4167 cal g^{-1} for spider silk reported in this study is thus perhaps rather high for an animal protein. This may be connected with the fact that, rather unusually for an animal protein, most of the amino acids comprising the silk protein molecule are simple ones with short side chains, such as glycine and alanine (Lucas, 1964; Lucas and Rudall, 1968; Peakall, 1964).

The value of 1.1577 J for the energy content of the silk of a web of 58.19 cm^2 must be added to the mean value of $724.46 \cdot 10^{-3}$ J for the respiratory energy costs of spinning a web of this size to produce the figure of 1.8822 J for the total energy cost of the production of such a web at any temperature. This figure represents 8.21 times the daily maintenance costs at 4.8° C, 5.25 times those at 10° C and 3.98 times those at 15° C.

The predation strategy of *L. zimmermanni* thus involves a considerable initial investment of energy in the production of a web for prey capture, though subsequent running costs are low. The efficiency of the strategy is dependent upon the life of the web in the wild.

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