

## Variables influencing laboratory energy budgets of *Geolycosa godeffroyi* (Araneae)

W. F. Humphreys

Departments of Zoology, Australian National University and La Trobe University

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The assimilation efficiency of food energy in *Geolycosa godeffroyi* (L. Koch) was unaffected by a series of constant temperatures, by a cyclical temperature regime or by spider weight above the first three instars. Assimilation efficiency varied directly with the feeding rate but within the range of feeding rates of field spiders the expected variation was less than 1%. Production had a caloric value consistent with assimilated food passing to fat storage. The characteristic relationship between weight and respiration was similar whether respiration was measured directly or indirectly through feeding experiments. Cyclical temperatures increased the respiration rate above the resting level and was cumulative with an increase in respiration resulting from feeding alone. More prey were killed under cycling temperatures than would be expected from the number killed at a series of constant temperatures. Feeding relationships were influenced by the number of prey presented at each feed and by behavioural interactions between the spider and the food species. Feeding ceased for a time before the moult, the period being directly related to the spider weight.

W. F. Humphreys, School of Biological Sciences, University of Bath, Bath BA2 7AY, England.

Ряд постоянных температур, колебания циклического температурного режима и вес пауков старше 3-го возраста не влияют на величину коэффициента ассимиляции энергии в пище у *Geolycosa godeffroyi* (L. Koch). Коэффициент ассимиляции находится в прямой зависимости от скорости питания, но в пределах нормальной интенсивности питания его колебания не превышают 1%. Калорийность продукции соответствует таковой ассимилированной пищи, используемой для накопления резервов. Характерная зависимость между весом и дыханием оставалась одинаковой при прямых и непрямых измерениях активности дыхания в экспериментах по исследованию питания. Циклический температурный режим повышает скорость дыхания по сравнению с уровнем основного обмена и воздействует также, как фактор пищевой активности, повышающий уровень активности дыхания. При циклическом температурном режиме пауки отлавливают большее количество жертв, чем при постоянных температурах. Количество жертв, доступных в период питания и взаимоотношения ловедения между пауками и их жертвами влияют на пищевые связи. Перед линькой питание прекращается, причем, этот период и определяет вес пауков.

## 1. Introduction

This paper is one of a series of background investigations providing detailed laboratory and field data for a study of the population energetics of the wolf spider *Geolycosa godeffroyi* (L. Koch) (Humphreys 1973, 1974, 1975abc, 1976, in press). The work has examined in detail the thermal regime of spiders in the field, and in laboratory studies, the influence of these cyclical temperature conditions on gross physiological parameters such as respiration, feeding and excretion.

The section of work reported here had a number of aims: –

1. Estimation of efficiencies unavailable from field data.
2. To determine whether these efficiencies were dependent on environmental temperature (both constant and cyclical), spider weight or feeding rate.
3. To measure the variation in efficiencies resulting from the use of gravimetric rather than caloric data.
4. To establish that indirect respiration estimates from feeding experiments had the same characteristics as direct measurements.

## 2. Methods

Spiders collected in the Australian Capital Territory were maintained in 300 ml plastic cups or 20 ml glass vials, according to their size, and provided with water daily. The spiders were fed a weighed amount of food every second day and that not ingested removed the next day. The larger spiders were fed on mealworms and the small ones on vestigial-winged *Drosophila melanogaster* Meig. If faeces were present the container was changed. The spiders were weighed at the start and end of the experiments which were from 13 to 22 d in duration. All weighings were performed to either 0.1 mg or to 0.001 mg according to the size of the sample. Food remains, exuvia, faeces and spiders were kept in a deep freeze at  $-15^{\circ}\text{C}$  until processed.

When required, the samples were dried to constant weight in a vacuum oven at  $35^{\circ}\text{C}$ . The vacuum oven had dry air slowly flowing through it. The energy content of the samples was measured on a Phillipson (1964) type micro-bomb calorimeter or a Gallenkamp ballistic bomb calorimeter according to the sample size. The instruments were calibrated using benzoic acid standards and no correction was made for endothermy (Paine 1966) or required for acid formation (Golley 1961). Individual samples were pressed into pellets before burning. Due to the inaccuracy of determining ash content from the residue in the calorimeter (Reiners and Reiners 1972), separate determinations of ash content were made by burning samples in a muffle furnace at  $550^{\circ}\text{C}$  for three hours (Cummins and Wuycheck 1971). Feeding experiments were conducted at  $10^{\circ}\text{C}$ ,  $15^{\circ}\text{C}$ ,  $20^{\circ}\text{C}$ ,  $30^{\circ}\text{C}$  and with the temperature cycling between  $11.7$  and  $29.3^{\circ}\text{C}$  (mean =  $20.2^{\circ}\text{C}$ ; see Humphreys 1975c) on a sine wave with a 24 h period.

Regressions relating the live weight to dry weight and dry weight to caloric value were prepared for all organisms used in the feeding experiments. Mean values were used for conversion if there was no significant variation in the ratios at different animal sizes, otherwise the regression equations were used to convert wet weight to dry weight and dry weight to caloric value.

Spiders ingest tissue in fluid form and discard most exoskeleton material so that it was necessary to determine the proportion of prey consumed (C; conventions after Petruszewicz and Macfadyen 1970) and the caloric value of the material not used (NU) to find caloric value of the food consumed ( $C + \text{NU} = \text{material removed}$ , MR). The weight and caloric value of faeces and excretions (FU) and exuvia were measured to estimate the caloric value of the food assimilated (A) and to add to production (P) estimates respectively. The change in spider live weight over the experimental period and the final caloric content were measured to find P and the caloric content of P; it is normally assumed that P has the same caloric value per unit weight as the entire animal (e.g. Reichle 1968, Shorthouse 1971, Edgar 1971) despite the artificial feeding conditions.

### *Excreta production*

Each cup that had been removed following excreta production was analysed for guanine, by the method described in Humphreys 1975a, and the relationship between guanine and the total excreta used to determine the weight of faeces produced. The spiders produced very little excreta and that produced was frequently difficult to collect because it was spread in a thin film around the container. The spectrophotometric method used here enabled the production of excreta by even the smallest spiders to be measured.

It is normally difficult to separate excretions from faeces in invertebrates and the practice has developed of pooling them as FU and calculating assimilation efficiencies accordingly. This practice is followed here. However wolf spiders produce a negligible quantity of faecal material owing to their external digestion. Much of the material measured as FU is guanine, the main nitrogenous excretory product of spiders (Schmidt et al. 1955, Atkinson and Chorlton 1956, Anderson 1966, Humphreys 1975a). The measure of C is consequently closer to A than is generally reported and the assimilation efficiency  $A/C$  is conservative.

### *Estimates of metabolic heat loss*

Metabolic heat loss was estimated in two ways. Firstly the respiration was calculated from the resting respiration rates at the appropriate temperature from the equations in Humphreys (1975c, in press). Secondly it was calculated by difference in the equation

$$\text{Respiration (R)} = C - \text{FU} - \text{P},$$

Where C, FU and P had been estimated in caloric terms during the feeding experiments. The ratio of the latter estimate to the former (Ra/Rr) is used for comparative purposes. An oxycaloric equivalent of 19.26J ml<sup>-1</sup> and a respiratory quotient of 0.75 were used where conversion was required.

### 3. Results and discussion

#### *Energy content of the various components.*

The live weight/dry weight/energy content relationships for all species used in the experiments are shown in Appendix 1. The values are in general agreement with the values for the same species or genus reported by Cummins and Wuycheck (1971). While some species show intraspecific variation in both energy and ash content with season (Wiegert 1965), no significant differences were detected between any of the subdivisions of the data for *G. godeffroyi*. The exuvia of *G. godeffroyi* had a mean caloric value of 23.25 J mg dry wt<sup>-1</sup> (S.E. = 1.21, n = 10). The latter compares with exuvia caloric values of 21.90, 22.83, 21.72 and 18.99 J mg<sup>-1</sup> in a scorpion (Shorthouse 1971), an elaterid, a cercopid (in Cummins and Wuycheck 1971) and a damselfly (Lawton 1971) respectively. Note that reports of caloric values in the literature expressed in calories are throughout this paper converted to joules (1 cal = 4.186J) for ease of comparison.

Pooled excreta samples were burnt in a calorimeter and had a mean energy content of 20.42 J mg<sup>-1</sup> (S.E. = 0.28, n = 8). This compares with 20.02 J mg<sup>-1</sup> in scorpion faeces (Shorthouse 1971) but is higher than other determinations for lycosid excreta of 15.35 J mg<sup>-1</sup> (Van Hook 1971) and 15.49J mg<sup>-1</sup> (Moulder and Reichle 1972); the energy content of the excreta of other groups is also low (Avery 1971, Lawton 1971).

Silk production was not determined quantitatively during the feeding experiments. Maximum silk production induced by frequently providing spiders with clean containers was 0.42 % of the spider caloric content per month; this compares with the cost of exuvia which account for between 8 and 24 % of production (Humphreys 1973, 1976). The low rate of silk production is consistent with the sedentary life led by these burrowing wolf spiders and the size of the glandulae ampullaceae which produce the drag line (Richter 1969, 1970).

The caloric value of production was determined at the conclusion of the feeding experiments when 22 of the spiders were dried and individually burnt in a calorimeter. These data differed from those used in the dry weight/caloric content conversion (Kruskal-Wallace test; H = 48.05, p < 0.001). The initial dry weight and caloric content of the spiders were estimated from the relationships in Appendix 1. The dry weight and caloric content of the spiders at the conclusion of the feeding experiments were measured directly. The caloric value of P during the feeding experiment was then determined from the relationship:

$$\frac{\text{Final caloric content (J)} - \text{initial caloric content (J)}}{\text{Final dry weight (mg)} - \text{initial dry weight (mg)}}$$

The caloric value of P was 37.85 J mg<sup>-1</sup> dry weight of production (S.E. = 2.355, n = 22). This compares with expected values of 39.15 J mg<sup>-1</sup> for fats, 16.33 J mg<sup>-1</sup> for animal protein and 23.65 J mg<sup>-1</sup> for carbohydrate. The value determined was thus consistent with the spiders storing fats in preparation for a subsequent moult (cf. 'freight' cost in Enders 1976). The value of 37.85 J mg<sup>-1</sup> was used to convert the estimated increase in dry weight of the spiders during the feeding experiments to energy units and effectively maximised

Tab. 1. Summary of feeding experiments run under various temperature regimes. The ratios are followed by their standard errors in parenthesis. M = mealworms and D = fruit flies as the food source. Individual results are contained in Humphreys 1973.

Temperature (°C)	Duration of experiment (days)	Food source	N	NU/MR	A/C	P/A	$\frac{C - FU - P}{R^*}$
20	16	M	7	0.115 (0.020)	0.892 (0.011)	0.525 (0.068)	1.74 (0.28)
30	15 or 16	M	12	0.134 (0.024)	0.891 (0.005)	0.496 (0.045)	1.89 (0.18)
Cycling	15 or 16	M	59	0.268 (0.025)	0.892 (0.004)	0.442 (0.027)	1.88† (0.09)
20	13 to 22	D	10	0.378 (0.022)	0.847 (0.028)	0.266 (0.051)	3.53 (0.69)
Cycling	14 or 22	D	33	0.250 (0.015)	0.794 (0.009)	0.592 (0.038)	1.19 (0.13)
Sum			123				
Mean				0.250	0.862	0.478	1.82

\* Estimate of resting metabolic heat loss for the same thermal conditions (spiders unfed) from direct respirometry (Humphreys 1975c, in press).

† This value become 2.54 when compared with the respiration rate at 20°C constant temperature (the mean of the cycling temperature; see text).

the estimate of production during these experiments and minimised that for respiration.

#### Feeding experiments

The results of the feeding experiments are summarised in Tab. 1. Few spiders ate in the 10°C and 15°C experiments and the results are not presented. Failure to eat at low temperatures is consistent with their biology for this species exhibits behavioural thermoregulation and maintains a body temperature close to 34°C on sunny days throughout the year (Humphreys 1973, 1974).

The data were analysed (after angular transformation) for the effect of different constant temperatures (20 and 30°C) and for the spider weight on the ratios (NU/MR and A/C) that were required for extrapolation to field conditions, production and consumption having been measured in the field (Humphreys 1975a, 1976). In the cycling temperature experiments the spider weight did not affect the ratios when mealworms were used as the food source ( $0.5 > p > 0.2$ ,  $n = 59$ ) but did when fruitflies were the food (NU/MR  $p < 0.001$ ; A/C  $p < 0.05$ ;  $n = 33$ ). The ratios obtained at different constant temperatures when mealworms were the food did not differ ( $p > 0.5$ ). The change in the ratios when fruitflies were used as the food source may be a developmental effect, as fruitflies were used for food only with the second and third instars; in lycosids the first instar is completed in the egg sac. These instars represent the period when the spiderlings change from reliance on yolk reserves to an independent predatory life so that major changes in feeding physiology may be expected. For technical reasons, however, the energy content of the smallest spiders was not measured at the conclusion of the experiments and the relationships indicated may be artefacts. These instars occupy only 5% of the life cycle of *G. godeffroyi* (Humphreys 1976) and they are discussed no further. As the cycling temperature experiment contains most of the data and more closely represents field conditions they will be considered below.

#### The effect of feeding rate on assimilation efficiency (A/C)

In the cycling temperature experiment with mealworms as food the assimilation efficiency (Y) varied with the rate of food consumption (XJ/spider live weight ( $\text{mg}^{0.8}$ )/day according to;

$$Y = 0.000075x + 0.873; n = 59; r = 0.32; t_s = 2.50, 0.02 > p > 0.01.$$

This indicates a variation in A/C from 0.88 to 0.93 over the range of feeding rates used in the experiments. Average feeding rates in the field over most of the size range of *G. godeffroyi* (2 to 2000 mg) varied from 0.91 to 1.19 J/spider live weight ( $\text{mg}^{0.8}$ )/day (Humphreys 1975a), giving an expected variation of A/C in the field from 0.890 to 0.896, or less than one percent.

An increase in assimilation efficiency at higher feeding rates is not unique (Davies 1963, 1964) but is certainly rare and is difficult to explain. It is not considered further here as the apparent assimilation efficiency in spiders, due to external digestion and subsequent ingestion mainly of fluids, is not comparable to those reported for most invertebrates.

The weight of the spiders, other than the first two free-living instars, constant temperatures of 20 and 30°C and cycling temperature between 12 and 29°C had no significant effect on the ratio A/C. Although the ratio varied slightly with feeding rate, the variation expected from actual field feeding rates was negligible. The various ratios calculated from the experiments are similar to those for other arachnids (Tab. 2) although the range of values found for different invertebrate carnivores varies widely (Lawton 1970: Tab. 14).

#### Comparison of respiration/weight relationships obtained by direct and by indirect respirometry

The relationship between an animals weight (X) and many physiological parameters (Y) is described by  $Y = aX^b$  where 'a' and the exponent 'b' are constants (otherwise expressed as  $\log_{10} Y = b \log_{10} X + a$ ). Respiration

Tab. 2. Comparison of the ratios NU/MR and FU/C found for *G. godeffroyi* with those reported in the literature for various arachnids.

Species	NU/MR %	FU/C %	Authority
<i>Geolycosa godeffroyi</i> (excluding the first three instars) .....	11.5–26.8	10.8–11.0	Present study
<i>Lycosa rabida</i> .....	16.0	9.2	Moulder and Reichle 1972
<i>Lycosa</i> sp. ....	–	7.0	Van Hook 1971
<i>Pardosa lugubris</i> .....	15.6–22.9	–	Edgar 1971
<i>Tarentula kochi</i> .....	58.6	–	Hagstrum 1970
<i>Urodacus yaschenkoi</i> (Birula) (Scorpionidae) .....	13.6–22.8	4.9–9.4	Shorthouse 1971

Tab. 3. Comparison of the exponent 'b' in the relationship  $y = ax^b$  where y represents some physiological measurement and x is the live weight of *G. godeffroyi*.

Method	Parameter	Temperature °C	Exponent (b)	Source
Feeding experiment .....	Joules	cyclic	0.802	this paper
Direct respirometry .....	oxygen	4, 10, 20, 30, 40	0.822	Humphreys 1975c
		cyclic	0.808	Humphreys 1975c
	carbon dioxide	4, 10, 20, 30, 40	0.806	Humphreys 1973
Food consumption .....	mg	field	0.761	Humphreys 1975a

tion in arthropods normally has an exponent between 0.70 and 0.85 (Edwards 1946, 1958, Scholander et al. 1953, Hemmingsen 1960).

The respiration from the feeding experiments can be derived indirectly from the relationship  $R = C - FU - P$  where, C, FU and P are known in caloric units. For the cycling temperature experiments with mealworms as the food item the relationship is;

$$Y = 0.802X + 0.0075, n = 59, r = 0.73, S.E. b = 0.100,$$

where  $Y = \log_{10} R (\mu l O_2 hr^{-1})$  and  $X = \text{weight (mg)}$ . The exponent of 0.802 is similar to those derived independently for *G. godeffroyi* (Tab. 3) by direct respirometry (Humphreys 1975c) as well as that derived from field estimates of food consumption (Humphreys 1975a). In addition the intercept 'a' of the equation is compatible with those obtained by direct respirometry. This is illustrated in Tab. 4 by examining the ratios resulting from comparison of regression lines derived under different experimental conditions using both direct and indirect respirometry. Comparison of line 1 with line 4 and of line 2 with lines 3  $\times$  4 shows that the magnitude of the changes in respiration levels caused by feeding and by cycling the temperature are similar whether measured directly in a respirometer or indirectly in a feeding experiment.

#### The effect of cyclical temperature on feeding parameters

The metabolic rates of spiders during the feeding experiments can be calculated from the relationship  $R = C$

–  $FU - P$  and compared with estimates for the resting respiration at the same temperature (mean temperature in cycling temperature experiments) derived from oxygen respirometry. This factor is  $1.74 \pm 0.28$  ( $n = 7$ ) for 20°C constant temperature and  $2.54 \pm 0.09$  ( $n = 59$ ) for cyclical temperature conditions when mealworms were the food source ( $t_{64} = 2.721$ ;  $0.01 > p > 0.001$ ). Cyclical temperatures result in a respiration level  $2.54/1.74 = 1.46$  of that under constant temperature conditions and this increase is cumulative with that resulting from the increased rate due to feeding. This value is close to that of 1.35 resulting from cyclic temperatures on resting spiders in oxygen respirometers (Humphreys 1975c).

Cyclical temperatures also influence the number of feeds taken by *G. godeffroyi*. When spiders were kept at a series of constant temperatures the number of mealworms consumed was linearly related to temperature between 10 and 30°C (Fig. 1). The number of feeds taken under cycling temperature conditions was greater than the number taken under constant conditions at 20°C ( $t_s = 1.726$ , one tailed test,  $0.05 > p > 0.025$ ; Wilcoxon two sample test with adjustment for tied values, Siegal 1956, Sokal and Rohlf 1969).

Three independent pieces of evidence support the effect of cyclic temperature on *G. godeffroyi*; direct respirometry described elsewhere (Humphreys 1975c), indirect respirometry from feeding experiments and the number of feeds taken.

#### The effect of food presentation

In some experiments conducted to produce a range of feeding rates (Humphreys 1975c) *G. godeffroyi* were

Tab. 4. Ratios resulting from the comparison of respiration rates of *G. godeffroyi* at several weights derived from various experimental treatments. RMR = resting metabolic rate.

Treatments compared	Spider live weight (mg)		
	10	100	1000
1. Fed and cyclic temperature <sup>1</sup> /RMR cyclic <sup>2</sup> .....	1.91	1.87	1.84
2. Fed and cyclic temperature <sup>1</sup> /RMR 20°C <sup>2</sup> .....	2.66	2.56	2.45
3. RMR cyclic <sup>2</sup> /RMR 20°C <sup>2</sup> .....	1.39	1.36	1.33
4. Fed 20°C <sup>2</sup> /RMR 20°C <sup>2</sup> .....	1.54	1.73	1.94

<sup>1</sup> Indirect respirometry where  $R = C - FU - P$ ; this paper.

<sup>2</sup> Direct oxygen respirometry; Humphreys 1975c, in press.

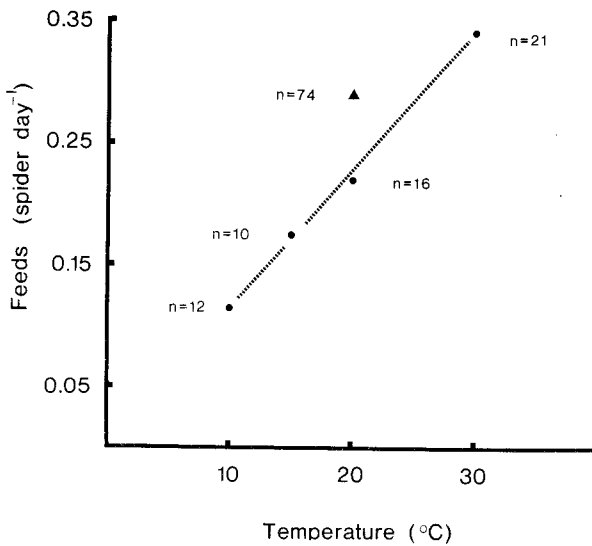


Fig. 1. The relationship between the mean number of prey killed by *Geolycosa godeffroyi* and the experimental temperature. The line joins the data from the two extremes of temperature. Circles represent data from the constant temperature experiments and triangles the experiment under cycling temperatures.

fed either bushflies (*Musca vetustissima* Walk.) or lycosids (*Alopecosa* sp. (*madigani* Hickman?), in different numbers (1 to 4) per meal. The number of prey killed, food consumption and respiration increased with number of food items presented when bushflies were the food but decreased when lycosids were fed to *G. godeffroyi* (Tab. 5). This inverse relationship to number of lycosid presented as food results from the interaction between the two lycosid species. When two lycosids of similar size meet (prey spiders were between 0.3 and 0.5 the size of *G. godeffroyi*) they interact with their forelegs and either retreat or the larger overcomes and eats the smaller. The scramble resulting from the addition of several prey in a confined space prevented normal interaction and when the spiders stopped moving they remained immobile in an almost cataleptic state; they were aroused only with difficulty but rapidly responded to the removal of the other spiders.

The time of food presentation in relation to the moult

is also important in the feeding experiments. Spiders do not eat for sometime before ecdysing (Miyashita 1968) and in *G. godeffroyi* this period was directly related to the weight of the spider. Under the cycling temperature conditions with mealworms as food the relationship was;

$$Y = 3.925X + 0.753;$$

$$r = 0.74, n = 21, t = 4.78, p < 0.001,$$

where Y = number of days during which the spiders did not eat prior to ecdysing and X = the spider weight (g).

#### Concluding remarks

The results underline the problems associated with the use of laboratory data to predict field events, for few variables are normally considered in the laboratory. They emphasise the necessity of concentrating on specific aspects of the energy budget as exemplified by the detailed studies of digestion in fishes (Brett and Higgs 1970) and invertebrate respiration (Phillipson 1962, 1963, Newell 1966, 1969, Newell and Pye 1971, Boyden 1972). Even under laboratory conditions, few studies have attempted to measure independently all the components of an energy budget. Teal (1957) calculated FU and NU from the values obtained for MR, P and R. Smalley (1960) considered that the sum of FU + P + R was equal to ingestion (C) when R was derived from respirometers and Edgar (1971) assumed that A/C was equal to 1.0 and determined R by substitution in the equation C = P + R. Shorthouse (1971) and Moulder and Reichle (1972) used similar methods to the present study but at one constant temperature.

Van Hook (1971) determined R in the laboratory from respirometry and by substitution in feeding experiments and used the ratio of the latter to the former to adjust the field estimates of R. The ratio is equivalent to my ratio  $\frac{C - FU - P}{R}$  where R is the resting metabolic rate in respirometers. The factor he obtained varied from 1.85 in *Pteronemobius fasciatus* (Gryllidae) to 3.57 in *Lycosa rabida* Walck. The latter factor is considerably greater than that obtained for *G. godeffroyi*, of 1.74 to 1.89, when mealworms were used as

Tab. 5. The relationship between the number of prey presented to *G. godeffroyi* at each feeding (X, n = 1 to 4) and various parameters (Y) over 14 days. Note the change from positive to negative correlation with the different prey types.

Food type	Parameter (Y)	Regression equation	Correlation coefficient	t-test against a slope of 0.0	N	
Bushflies	Number of prey killed	$y = 6.86X + 0.22$	1.00	83.0	$p < 0.001$	10
	Consumption ( $J g^{-1}$ )	$Y = 2039.0X + 547.6$	0.65	2.4	$0.05 > p > 0.02$	10
	Respiration ( $J g^{-1}$ )	$Y = 936.2X + 688.3$	0.68	2.64	$0.05 > p > 0.02$	10
	$R = C - P - FU$					
Lycosids	Number of prey killed	$Y = -1.40X + 6.76$	-0.88	8.36	$p < 0.001$	9
	Consumption ( $J g^{-1}$ )	$Y = -1627.4X + 4028.4$	-0.84	4.08	$0.01 > p > 0.001$	9
	Respiration ( $J g^{-1}$ )	$Y = -735.6X + 2348.7$	-0.67	2.36	$0.05 > p > 0.02$	9
	$R = C - P - FU$					

the food source. Van Hook did not determine the caloric value of production and as his experimental conditions were similar to those used for *G. godeffroyi* it is possible that some of the difference is due to his having underestimated P. In the case of *G. godeffroyi* under the cycling temperature conditions, the assumption that any increase in weight during the feeding experiments was of equivalent caloric value to the whole spider would have raised the factor from 1.88 to 2.41, which is 128 % of the actual value.

Within this study the magnitude of the effect of various assumptions can be assessed. I will consider only the caloric value of the components measured during feeding experiments. The assumption of equivalent caloric value for all components or that the caloric value of growth (or storage) is equivalent to that of the whole animal may lead to wide variations in various efficiency indices (Tab. 6).

The effects discussed above may influence the validity of extrapolating laboratory feeding experiments to the field. Where feeding relationships have been examined in detail, the simple relationships derived from the one temperature, one prey and short duration feeding experiments that are frequently used in energetics studies have not been confirmed. In salmon the mean size, conversion efficiency and digestion rate were markedly influenced by temperature (Brett and Higgs 1970). In *Pyrrosoma nymphula* (Sulzer) the effects of meal size and temperature could be effectively ignored as far as energetics was concerned but the prey type could have marked effects (Lawton 1970). In the diplopod *Sarmatiulus kessleri* Lohmander both the rate of food consumption and the assimilation efficiency (FU/C) were influenced by temperature in the same general manner. Both curves had minima at 5°C and 32°C but below and above this temperature range both increased abruptly and considerably (Striganova 1972).

There was no evidence from laboratory experiments with *G. godeffroyi* that the weight of the spiders, above the first three instars, or temperature had any effect on the efficiencies measured. Moulder and Reichle (1972) found that in a population of spiders, the assimilation efficiency (A/C) varied with season from 90.4 % in summer to 99.1 % in winter. It is not clear how they

derived this variation, as they used a constant laboratory determined assimilation efficiency (loc. cit: 491).

The increase in respiration following feeding may partly be accounted for by the effect of 'specific dynamic action' (Brody 1964, McGilvery 1970: 522). Considering the high protein diet of spiders, the effect would be maximised but it is unlikely to account for the almost 2-fold increase in respiration following feeding in *G. godeffroyi* and other lycosids (Itô 1964, Miyashita 1969, Hagstrum 1970, Nakamura 1972, Myrcha and Stejgwill-Laudańska 1973, Humphreys in press). Lycosids are opportunistic predators and the facility of lowering maintenance costs during periods of low food availability may have considerable adaptive advantage. Conversely a 3-fold increase in respiration following feeding would bring the RMR of *G. godeffroyi* to the level expected from Hemmingsen's (1960) respiration/weight relationship for all ectothermic animals, so that after feeding the spiders would be operating at a similar level of metabolic activity to other ectothermic animals.

#### Appendix 1:

The water and energy content of various species used in the feeding experiments.

Mealworms;

$Y = 0.395X - 0.571$ ;  $r = 0.994$ , SEb = 0.005, n = 75;

where Y = dry weight (mg) and X = wet weight (mg).

$Y = 26.88X \div 28.36$ ;  $r = 0.994$ , SEb = 0.456, N = 21;

where Y = Joules and X = dry weight (mg).

NU when food was mealworms = 25.21 J mg<sup>-1</sup> (SE =

0.46, n = 53).

Fruit flies (pooled samples);

$Y = 0.269X + 0.0005$ ;  $r = 0.996$ , n = 8; where Y = dry weight (mg) and X = wet weight (mg).

Energy content 23.78J mg<sup>-1</sup> (SE = 0.253, n = 5).

NU when food was fruit flies = 18.96J mg<sup>-1</sup> (SE = 0.242, n = 3).

Tab. 6. Comparison of various ecologically significant efficiencies determined on a caloric basis, a gravimetric basis and assuming that the caloric value of production (P) was equal to the whole spider caloric value per unit weight.

Condition used in calculation	$\frac{NU}{MR}$	$\frac{A}{C}$	$\frac{P}{C}$	$\frac{P}{A}$	$\frac{C - FU - P}{R^1}$
All values caloric .....	0.268	0.891	0.395	0.442	1.88
P & spider caloric value equal .....	-	-	0.254	0.284	2.41
Gravimetric .....	0.273	0.861	0.273	0.314	2.09 <sup>2</sup>
Maximum variation (%) .....	1.9	3.5	55.5	55.6	28.2

<sup>1</sup> Estimates from respiratory data on resting animals at the appropriate temperature (Humphreys 1975c, in press).

<sup>2</sup> Gravimetric and then assumed all caloric values = whole spider values.

*G. godeffroyi*;

$Y = 0.285X - 0.20$ ,  $r = 0.989$ ;  $SE_b = 0.005$ ,  $SE_a = 0.20$ ,  $n = 82$ , where  $X =$  wet weight (mg) and  $Y =$  dry weight (mg).

	Caloric content (J mg dry wt <sup>-1</sup> )		
	Mean	S.E.	N
All samples . . . . .	24.31	0.415	63
Oct - April . . . . .	24.62	0.561	30
May - Sept . . . . .	23.74	0.635	33
Less than 50 mg dry wt .	23.25	0.103	19
Males . . . . .	22.80	0.622	8
Spiderlings (pooled) . . . . .	21.84	0.374	5

	Ash (% dry wt)		
	Mean	S.E.	N
May - Sept . . . . .	7.15		18
Oct - April . . . . .	7.02		23
Year . . . . .	7.08	0.177	41

J mg ash free dry wt<sup>-1</sup> for all year = 26.37

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