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ECOLOGICAL ENERGETICS OF *GEOLYCOSA GODEFFROYI* (ARANEAE: LYCOSIDAE) WITH AN APPRAISAL OF PRODUCTION EFFICIENCY IN ECTOTHERMIC ANIMALS

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SUMMARY

(1) This study derives a series of energy budgets for the burrow inhabiting wolf spider *Geolycosa godeffroyi* (Koch) in the Australian Capital Territory.

(2) It examines the relationship between energy budgets derived by the extrapolation of various laboratory measurements of respiration rate with those derived independently by measuring consumption in the field in addition to production.

(3) The lowest possible respiration rate (resting metabolic rate) is determined over the entire size and temperature range found in the field and takes account of the sophisticated behavioural thermoregulation shown by the spiders.

(4) The increase in respiration rate due to a number of variables is determined. These include nutritional state, reproductive condition, size, temperature cycles, season, acclimation and sex. The increase in respiration due to many of these factors is cumulative.

(5) On extrapolation to field conditions using actual spiders' temperatures the estimated metabolic heat loss varied by at least 2.5 times according to the type of respiration data used.

(6) From a knowledge of the effect of some variables on respiration rate it is argued that the respiration rate in the field should be about three times the resting metabolic rate.

(7) Budgets derived using field measurements of both production and consumption give respiration estimates between 3 and 4 times the resting metabolic rate.

(8) Budgets derived using the higher respiration rates are in accord with those for other spiders derived by different techniques.

(9) The effect of different types of respiration estimates on published energy budgets is considered in detail.

(10) It is suggested that the methodologies used to derive energy budgets have a gross influence on the estimates of metabolic heat loss and introduce considerable bias.

(11) When the methodologies are considered it is doubtful that some of the generalizations about production efficiency that have been proposed can be substantiated.

INTRODUCTION

Despite the increasing number of publications in ecological energetics few studies have measured independently more than one component of the budget, usually production (P), in the field. Metabolic heat loss (R) is commonly added to P (which is often considerably smaller than R) and the remainder of the budget derived. R is traditionally estimated by

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measuring respiration rate in the laboratory and extrapolated to the field. On extrapolation correction may or may not be made for weight, population structure, temperature, acclimation, seasonal variation, salinity, humidity and activity and for nutritional, moulting or reproductive state, etc. Otherwise some arbitrary factor may be used to adjust respiration rates to account for 'field activity', most commonly the factor 2.0 is used as suggested for fishes by Winberg (1956). This extrapolation is crucial as measured respiration rates may differ markedly according to the experimental conditions; estimates may vary more than six fold in coleoptera (Hågvar 1975) and spiders (Humphreys 1977a, b) or by nearly two orders of magnitude in fishes (Weatherley 1972).

Although the problems involved in estimating metabolic heat loss in field populations have been exhaustively discussed (e.g. Cameron, Kostoris & Penhale 1973; Streit 1976), little attempt has been made to explain the differences found by various methods. The present study examines the relationship between energy budgets derived using laboratory respiration data and those derived independently by the measurement of consumption, in addition to production, in the field population. The laboratory studies attempt to relate respiration to the qualitative and quantitative environmental variation experienced by spiders in the field.

A wide range of energy budgets can be derived according to the types of respiration data considered. Various generalizations about production efficiency that have been proposed in the literature are discussed in relation to the variability found in the budgets presented here.

METHODS AND RESULTS

Much of the methodology and many of the basic data required to derive the energy budget for *Geolycosa godeffroyi* (Koch) have been analysed and discussed elsewhere in the context of budget estimates (Humphreys 1974, 1975a, b, c, 1976, 1977a, b, 1978). Synopses of the methodologies and the relevant results are given here where appropriate to establish the approach adopted in this study and as a measure of the rigour of the work. Readers are referred to the appropriate papers and to specific Figures and Tables to facilitate comparison and amplify the synopses presented here. The conventions used for components of the energy budget follow Petrusewicz & Macfadyen (1970); namely *MR* (material removed), *NU* (material not used), *C* (consumption), *A* (assimilation), *FU* (rejecta; faeces and urine), *R* (respiration), *P* (production), *E* (elimination) and ΔB (change in biomass); where $MR = C + NU$, $C = A + FU$, $A = C - FU = P + R$, $P = E + \Delta B$, all expressed in caloric units. Where necessary caloric measures from the literature expressed in calories are converted to joules (1 calorie = 4.186 J; 1000 J = 1 kJ).

Field work was conducted in a strip cleared of trees through the Kowan Forest Reserve in the Australian Capital Territory (Humphreys 1976). All data refer to the whole population on the 1330 m² field site unless specified. Unless stated, throughout the paper mean values are presented with their standard errors.

Population biology

G. godeffroyi is burrow inhabiting for much of its life and uses the burrow mouth as the focus of the hunting and behavioural thermoregulation activities. The spiders maintained body temperatures of about 35 °C whenever sufficient solar radiation was available, they had adequate access to food and water and were in a non-breeding condition. The preferred temperature fell to about 30 °C when carrying egg sacs or deprived of food or water (Humphreys 1974, 1978). Egg sacs contained between 180 and 1094 eggs and were

heaviest at the time of peak egg sac production in February. The spiderlings emerged from the egg sacs after 3.6 ± 1.1 weeks ($n = 14$) and were carried on the backs of the females for 8.6 ± 2.3 days ($n = 11$) before dispersing and starting to feed. Spiders from egg sacs laid in February had reached size classes 5 to 7 by the winter by which time they were all burrow dwelling. They reached the penultimate instar (size class 13 or 14) by their second winter and bred the following summer. Males senesced and died after mating and the females laid one or two egg sacs and were probably all dead by mid-winter (August) following breeding.

The population size, size class duration and growth rates (Humphreys 1976, Table 7, Fig. 2) were determined by regular field sampling, not involving removal, of a marked population between May 1971 and November 1972 at 4-weekly intervals, rising to 6 weeks during the winter of 1972. The data required for the energy budget are calculated for the period of 16 October 1971 to 14 October 1972 (365 days). Fifteen size classes, which closely approximated instars, were derived on the basis of field derived growth increments between instars. The mean live weight of size class 1 was 2.48 mg and of size class 15 females was 1543 mg. The duration of size classes varied between 12.5 days in size class 1 to 201 days in size class 14 with a summer range of size classes 2 to 12 of between 18 and 33 days.

Synopses of the numbers of spiders passing through each size class for the relevant year and in each month are given in Tables 1 and 2 (details in Humphreys 1976, Table 10). The numbers passing through the size classes are used rather than the actual numbers of spiders to take account of the different size class duration seasonally and between size classes (cf. Winberg 1971) and was calculated as: Number of spider days/Duration of size class.

On a semilog plot a fairly linear size class specific survivorship curve was found for *G. godeffroyi* (Type III; Slobodkin 1961) indicating a roughly constant mortality per size class (Humphreys 1976, Fig. 6). The relationship is adequately described by the equation

$$\log_{10} Y = 3.770 - 0.181X; \text{ S.E. } b = 0.013, r = 0.97$$

where Y represents the number of spiders passing through size class X over the year. Budgets will be presented for the actual population data and for those described by the above equation which will be referred to as the 'model population'.

Standing crop

The mean standing crop for each size class and month is given in Tables 1 and 2 respectively and the change in standing crop between October 1971 and October 1972 in Table 1. The standing crop fell over the year by 3.98 kJ or 12.8% with the fall attributable to the larger size classes that had overwintered during the severe winter of 1971. The mean annual standing crop for the entire field site was 284.19 kJ or 214J m⁻² (8.9 mg dry wt m⁻²). Adult females represented 39.1% of the standing crop but only 0.17% of the number of recruits to all size classes. The first seven size classes represented 22.3% of the standing crop but 96.6% of the number of spiders passing through all size classes.

Exuvia production

Exuvia collected from all size classes had a mean caloric value of 23.25 ± 1.21 J mg dry wt⁻¹ ($n = 10$, pooled samples). Exuvia loss constituted 9.8% of total production and varied from 8.2% to 23.9% in the different size classes; the larger spiders lost proportionately more energy in exuvia than smaller spiders. These values compare with a total cost of

TABLE 1. Synopses of various ecological parameters for each size class of *Geolycosa godeffroyi* from October 1971 to September 1972

Size class	Number passing through size class	Mean standing crop ($J \times 10^{-3}$)	Exuvia production ($J \times 10^{-3}$)	Exuvia/P	Production ($J \times 10^{-3}$)	Food consumption in field ($J \times 10^{-3}$)	Resting metabolic heat loss ($J \times 10^{-3}$)	Seasonally adjusted metabolic heat loss ($J \times 10^{-3}$)	Change in standing crop Oct. 1971-Oct. 1972 ($J \times 10^{-3}$)
Spiderlings	7446								
1	5852	3.38	4.04	0.082	49.27	145.62	28.17		0.00
2	2088	4.53	2.36	0.156	15.14	182.67	26.63		0.02
3	1522	4.54	2.85	0.100	28.39	150.17	24.53		0.08
4	682	5.32	1.93	0.126	15.35	117.12	20.94	283.91	-5.90
5	497	7.81	2.49	0.112	22.30	221.33	31.01		-0.43
6	953	16.55	7.86	0.116	68.10	463.17	63.25		-13.81
7	816	21.24	11.07	0.156	71.17	446.45	78.23		20.09
8	60.1	2.87	1.34	0.183	7.35	76.91	10.44		-0.01
9	99.0	4.63	3.63	0.146	24.83	91.67	15.63		-1.09
10	101.6	7.04	6.13	0.179	34.16	126.48	23.89		-0.81
11	79.2	7.92	7.86	0.147	53.57	128.67	26.26		0.01
12	28.5	11.37	4.65	0.193	24.11	67.13	15.97	459.97	4.02
13	37.0	24.00	9.88	0.214	46.11	309.79	73.37		-16.10
14	16.4	51.94	5.08	0.239	21.25	501.93	99.11		-8.72
15	12.7	111.06			53.02	949.26	206.90		-17.19
Eggs					183.51				
Silk					8.97				
Sum	20291	284.2 = 0.214 m ⁻²	71.2		726.6	3978.4	744.3	743.9	-39.84

TABLE 2. Monthly synopses of various ecological parameters for the population of *Geolycosa godeffroyi*

	Number passing through size classes	Standing crop ($J \times 10^{-3}$)	Production ($J \times 10^{-3}$)	Food consumption in field ($J \times 10^{-3}$)	Resting metabolic heat loss ($J \times 10^{-3}$)	Seasonally adjusted metabolic heat loss ($J \times 10^{-3}$)
Oct. 1971	306.4	311.44	48.51	209.1	44.61	44.26
Nov.	892.6	339.43	74.05	320.8	70.88	67.65
Dec.	1844.4	297.26	96.51	397.5	83.44	76.79
Jan. 1972	5467.7	253.63	158.45	326.6	72.52	66.74
Feb.	2610.7	268.46	63.40	323.8	59.78	57.06
March	3398.9	219.89	64.70	209.0	76.12	75.69
April	2866.9	294.72	89.39	165.6	104.85	108.20
May	2167.9	306.44	81.08	682.7	82.46	87.50
June	276.2	252.03	12.67	483.4	38.63	42.90
July/Aug.	299.3	295.90	20.85	527.4	51.46	55.85
Sept.	159.5	286.94	16.96	332.3	59.59	61.27
Oct.		271.60				
	$\Sigma 20291$	$\bar{x} = 284.2$	$\Sigma 726.6$	$\Sigma 3978.4$	$\Sigma 744.3$	$\Sigma 743.9$

exuvia production expressed as a percentage of total production of 9.4% in a lycosid (Edgar 1971), 8.8% in a scorpion (Shorthouse 1971), between 4.2 and 4.3% in a dipteran (Stockner 1971), and between 8.4 and 12.6% in larvae of a damselfly (Lawton 1971).

Production

Production by size class N was calculated as the difference in mean caloric content between size class N and $N-1$ plus the exuvia shed by size class $N-1$ (Table 1). Population production was calculated as the number passing through the size class times the caloric change between size classes and summed for all size classes in each month for the year save for size classes 1 and adult females (either size class 14 or 15). Size class 1 production was calculated as the difference in caloric content between free-living size class 1 spiders and those found on the backs of females. All females were considered to grow to 1200 mg excluding reproduction; this weight being close to the mean weight of females following the production of second egg sacs in the field (1195 ± 97.7 mg, $n=7$). Only females gamete production was considered as males contribute little in caloric terms. Egg production was estimated from the weight of egg sacs in the field at 7446 eggs (mean 338 eggs per egg sac, Humphreys 1976) with a caloric content of 24.7 ± 0.26 J per egg ($n=5$ pooled samples of 50 eggs) giving a total egg production of 183.5 kJ. The silk of the egg sacs had a mean weight of 22.2 ± 3.51 mg ($n=7$) with a caloric content of 18.4 ± 1.34 J mg dry wt⁻¹ ($n=10$). Twenty-two egg sacs were produced during the year giving a cost of 8.97 kJ for egg sac silk and a total reproductive cost of 192.5 kJ. *G. godeffroyi* produced a negligible amount of silk for other purposes (Humphreys 1977a).

Elimination

Elimination was calculated by two methods. First as production minus change in standing crop ($E = P - \Delta B$) between October 1971 and October 1972 (Table 1) giving $726.6 - (-39.8) = 766.4$ kJ. Secondly it was derived directly from the estimated size class specific survivorship curve for *G. godeffroyi* (actual not model curve in Humphreys 1976; Fig. 6). The change in numbers passing through size classes N and $N-1$ was multiplied

by the mean caloric content of size class N and cumulated for all size classes. The mean caloric content of females was taken from post reproductive individuals and the elimination from reproduction as the caloric content of eggs plus egg sacs minus the caloric content of the resulting spiderlings, giving a total elimination of 754.1 kJ, a value in reasonable agreement with the previous estimate.

Food consumption in the field

A method has been described to estimate the food consumption of *G. godeffroyi* in the field (Humphreys 1975a); it was based on a calibration curve relating the food consumed in 14 days to the production of components of the excreta (mainly guanine and hereafter referred to as 'guanine') during the subsequent 7 days. The calibration curve was obtained in the laboratory under a wide range of conditions including prey type varying in major nitrogenous excretory product, feeding rate, at 10, 20 and 30 °C and with temperature cycling between about 10 and 34 °C on a sine wave to simulate field conditions. The final equation relating 'guanine' production to spider weight and food consumption accounted for 85.3% of the variance ($P < 0.001$, $n = 76$; Humphreys 1975a, Table 4). Prey, arachnids and insects (Humphreys 1973), were assumed to have a mean caloric content of 21.52 J mg dry wt⁻¹ (Cummins & Wuycheck 1971, p. 33). Field testing showed that the method was reliable within the range of conditions used to derive the calibration curve where temperature > 10 °C. Despite effective behavioural thermoregulation by *G. godeffroyi* (Humphreys 1974, 1978) mean spider temperatures dropped below 10 °C at Kowan between June and August 1972; spiders would not feed at constant temperatures below 10 °C (Humphreys 1977a).

Spiders were collected from the field throughout the study, returned to the laboratory and maintained with water but not fed for 7 days at 20 °C after which the 'guanine' produced was measured (Humphreys 1975a). For each month a regression relating spider weight (< 800 mg) to 'guanine' production was derived and for adult spiders (> 800 mg) the mean 'guanine' production calculated. These relationships were used to calculate the mean food consumption of each size class of *G. godeffroyi* in each month (Humphreys 1975a, Tables 8 and 9). The food consumption of the population was derived from the mean daily food consumption of the size class times number passing through that size class times size class duration in that month; estimates were made for all size classes in each month and summed for the year.

While synopses of food consumption are given for each size class and month (Tables 1 and 2), the winter period will be excluded in the calculation of some energy budgets (specified below) as the mean spider temperature was outside the limits used to derive the calibration curve; in these months the spiders could not fully thermoregulate (Humphreys 1978), some showed negative production (Humphreys 1973) and yet the method indicated high consumption.

Various efficiencies

Two measures of efficiency could not be derived in the field, namely NU/MR and A/C , and were derived from detailed laboratory energy budgets; these have been described and the variables affecting them discussed (Humphreys 1977a). Feeding experiments were conducted on the complete size range of *G. godeffroyi* measuring all components of the budget save respiration, which was derived by difference. Experiments were conducted using two prey species and at a series of constant temperatures (10, 20 and 30 °C) and with a cycling temperature regime. The caloric value of production was measured and indi-

cated that weight increase was due to fat storage; this had a marked effect on other estimates and effectively maximized the estimate for P and minimized that for R (Humphreys 1977a).

The weight of the spiders (other than the first three of 15 size classes in which the caloric value of P could not be determined for technical reasons) and temperature had no significant effect on the ratios NU/MR and A/C . In addition cycling temperatures on a sine wave with a 24 h period between 11.7 ± 0.65 °C and 29.3 ± 0.14 °C did not significantly change the ratios thus allowing some confidence in extrapolating these critical ratios to the field. Assimilation efficiency (A/C) was directly related to feeding rate ($0.02 > P > 0.01$) varying from 0.88 to 0.93 over the range of feeding rates used. The range of feeding rates found in the field (Humphreys 1975a) would give an expected variation in A/C between 0.890 and 0.896, less than 1% (Humphreys 1977a).

The ratios used for the energy budgets are those from the cycling temperatures experiments for which most data are available and which most closely represents conditions in the field; these gave $NU/MR = 0.268 \pm 0.0245$ and $A/C = 0.892 \pm 0.0042$ ($n = 61$) for experiments of 15 or 16 days duration. These values approximate those obtained for other lycosids (see Humphreys 1977a, Table 2).

Spider temperatures

Any necessary extrapolation of laboratory derived temperature dependent data to field conditions requires detailed knowledge of the animals thermal regime. In aquatic ectotherms the problems are often simple and a knowledge of temperature change in the water body may suffice. In terrestrial situations steep thermal gradients may occur, particularly at the interfaces (Burrage 1971) where most small organisms live. Only the most detailed knowledge of an organisms movements and of its microenvironment will adequately describe its thermal environment (Bursell 1964; Macfadyen 1967); even this may not be adequate if the organisms use sophisticated thermoregulatory behaviour of the type found in *G. godeffroyi* (Humphreys 1974, 1978) and many lizard species (Huey & Slatkin 1976).

In the field at Kowan, body temperatures of *G. godeffroyi* were recorded continuously throughout the day and at intervals through the year using implanted thermocouples (Humphreys 1974, 1978); the technique permitted spiders free movement through their available thermal environment, complex behaviour such as egg sac construction, and gave similar results to those obtained by telemetry which involved no attached leads (Humphreys 1978). To calculate various field rate processes the temperature for each 0.25 h was recorded throughout the day and the relevant parameter calculated for each 0.25 h interval for each size class and summed over 24 h for each day spider temperature data were available (26) and the mean daily total for each month determined.

Metabolic heat loss

Respiration, as an index of metabolic heat loss, can rarely be measured directly in natural populations, yet it is the largest component of an energy budget requiring extrapolation from laboratory to field animals. Furthermore it is the parameter most prone to vacillate according to the experimental situation or the state of the animal. Accordingly considerable attention has been given in this study to the measurement of respiration to determine how estimates of R from field measurements ($A - P$) relate to those derived from laboratory respirometry. Direct measurements from respirometers

and indirect measurement of respiration from laboratory energy budgets have been presented and analysed elsewhere (Humphreys 1975b, 1977a, b).

The approach adopted in this study was to determine the lowest measure of respiration, the resting metabolic rate (R_r), and to determine departures (R_a) from this rate under a variety of experimental conditions. The derived factor R_a/R_r is used to measure the possible range of respiration rates under conditions closer to those found in the field. The R_r was determined on spiders acclimated at the experimental temperature for 7 to 10 days and watered but not fed and measured in a tubular chamber of dimensions similar to the spider's burrow and in which the spider remained largely immobile.

Direct respirometry was conducted in electrolytic respirometers (Humphreys 1973) over 24 h to include variation due to diurnal rhythm. Measurements were made over the entire size range of *G. godeffroyi* at various times of the year and at 4, 10, 20, 30 and 40 °C. A multiple regression model based on 258 spiders was derived relating the R_r to spider weight, temperature and season which accounted for 95.3% of the variance (Humphreys 1977b). Spider temperatures in the field were used with the regression model to calculate R_r for each 0.25 h interval over 26 days for which field temperatures of spiders were available. The mean daily R_r for each month was calculated for each size class of *G. godeffroyi* and multiplied by the number of spiders passing through that size class and the size class duration in that month. Estimates were summed for each size class and month to give the annual resting respiration of the population (Tables 1 and 2).

Actual spider temperatures gave an estimated annual respiration 52% greater than the use of mean daily ambient air temperatures and the former measure gave an estimate similar to that derived using mean monthly maximum air temperature (Humphreys 1977b, Fig. 2); all budget estimates of respiration were derived using actual spider temperatures and multiplied by a factor where appropriate (see below) to give a measure of active respiration more appropriate to field conditions.

Additional experiments were conducted to determine the effects on respiration (numbers of spiders in parentheses) of feeding (55), sex (24), activity, acclimation (49) (Humphreys 1977b) and cycling temperatures (53) (Humphreys 1975b). Where appropriate these data were compared with those derived indirectly from laboratory energy budgets used in the section 'various efficiencies' and detailed elsewhere (Humphreys 1977a). To derive factors by which treatments altered respiration rate from the resting level the weight/rate regressions were compared with those for the resting metabolic rate at the same temperature.

The following conditions increased the respiration rate of *G. godeffroyi* above the resting level by the factor (R_a/R_r) in parentheses; cycling temperature (1.35) (Humphreys 1975b), activity (2.0–4.9), feeding (1.59–2.19), seasonal variation (1.2) (Humphreys 1977b). Furthermore the effects were cumulative so introducing a potential error factor of at least 5–15. This factor could be increased by 1.52 (= 7.83) on extrapolation to the field if ambient rather than spider temperature data were used. The existence and magnitude of the effects of cycling temperature, feeding and the cumulative effect mentioned were supported by indirect respiration estimates from laboratory energy budgets (Humphreys 1977a).

The magnitude of the various treatment effects is supported by scattered evidence in the literature but not previously established for one species (Humphreys 1975b). Subtle interspecific interactions may have marked effects on the laboratory energy budget of *G. godeffroyi* (Humphreys 1977b, Table 5) and they need interpreting with caution. In addition the period without feeding prior to the moult was longer in larger *G. godeffroyi*

(Humphreys 1977b) whereas the stadia duration was size class dependent; these factors may bias the results of laboratory feeding experiments especially as spiders brought into the laboratory appear to be induced to moult.

Direct measurements of respiratory quotients were not made for *G. godeffroyi* as a soda lime barrier was used to eliminate any ozone formed by electrolytic oxygen generation in the respirometers. Separate measurements of carbon dioxide production by *G. godeffroyi*, under the same acclimation regimes and temperatures used for oxygen respirometry, were made for 24 h periods using a flowing air technique in line with an infra red analyser (Humphreys 1973). Probably due to movement of animals within the chamber this technique produced greater variability in the data than those derived from oxygen measurements. Data from 4 and 10 °C were comparable with those from oxygen respirometry (homogeneous variance) and gave a mean respiratory quotient of 0.749 ($n=26$). A respiratory quotient of 0.75, indicative of mixed protein and fat diet, is used throughout this study and an oxy-caloric coefficient of 19.26 J ml O₂⁻¹ at N.T.P.

Derivation of energy budgets

In this section a series of energy budgets is derived using information from different sources and under various assumptions. Budgets are initially derived using field data for *P* and combined with various laboratory respiration estimates using spider temperature data from the field. These are compared with other budgets derived using field estimates for both *P* and *C*. In all budgets the ratio $A/C=0.892$ being that obtained under cycling temperature conditions in the laboratory.

Laboratory resting metabolic rate data are combined with spider temperature data from the field, and population size and structure to obtain the estimated resting metabolic heat loss in the field (*Rr*). Any other derivation of population metabolic heat loss is denoted *Ra* and the ratios Ra/Rr and P/A used for comparative purposes.

In block Z of Table 3 the field estimated *P* is combined with *Rr* to give the minimum possible energy budget for *G. godeffroyi*. In Z, 1-3 *A* is calculated as $P + Ra$ and divided by the assimilation efficiency to give *C*. Budgets are presented for the whole population (Z1), and both the smaller (Z2) and larger (Z3) size classes. For the population $P/A=0.49$. In budget Z4 the estimate *Rr* is multiplied by the factor 1.883 to account for the increase in respiration found in the laboratory when the spiders were fed every 2 days. The other values were derived as for Z3 and gave $Ra/Rr=1.88$ and $P/A=0.34$. The increased respiration rate in lycosids following feeding is well founded (Miyashita 1969; Hagstrum 1970b, Nakamura 1972, Humphreys 1977a, b, 1978). Using conservative assumptions about average prey size *G. godeffroyi* would have to feed on average every 1.5 to 6.8 days according to size class (Humphreys 1975a, Table 10).

In budget Z5 the value for *Ra* in budget Z4 is multiplied by 1.35 to account for the increase in respiration in *G. godeffroyi* under conditions of cycling temperature (Humphreys 1975b); this effect was cumulative with the increase above resting metabolic rate caused by feeding (Humphreys 1977a). Of the budgets derived using laboratory derived respiration rates Z5 is the most representative of conditions in the field and Ra/Rr and P/A were 2.54 and 0.277 respectively.

Of the other factors found to change respiration in the laboratory, seasonal variation is incorporated in the regression model to calculate *Rr*, and activity, which had a major effect, was a transitory response and *G. godeffroyi* was more or less sedentary in the field (Humphreys 1978); activity would increase respiration in the field but to a small and unknown extent.

TABLE 3. Synopsis of annual population energy budgets for *Geolycosa godeffroyi* calculated as described in the text

Budget	Procedure used in calculation*	P	Rr	C	A	Ra	Ra/Rr	P/A
Laboratory Rr or Ra								
Z1	All size classes	726.6	<u>744.3</u>	1649.0	1470.9	<u>744.3</u>	1.0	0.494
Z2	Size classes 1-8	277.1	<u>283.2</u>	628.1	560.3	<u>283.2</u>	1.0	0.495
Z3	Size classes 9-15	449.5	<u>461.1</u>	1020.9	910.6	<u>461.1</u>	1.0	0.494
Z4	All size classes: Ra = Rr × 1.883 for effect of feeding	726.6	<u>744.3</u>	2385.8	2128.1	<u>1401.5</u>	1.88	0.341
Z5	Ra of Z4 × 1.35 for effect of cycling temperature	726.6	<u>744.3</u>	2935.7	2618.6	<u>1892.0</u>	2.54	0.277
Field consumption included								
Y1	All size classes	726.6	<u>744.3</u>	3978.1	3548.5	2821.9	3.79	0.205
Y2	Hatch February 24: individual female	23.55	<u>23.5</u>	121.6	108.5	84.9	3.61	0.217
Y3	Hatch February 24: model population	632.0	<u>620.6</u>	3112.5	3112.5	2480.5	4.00	0.203
Summer Ra/Rr used to calculate winter R and C								
X	All size classes	726.6	<u>744.3</u>	3306.5	2949.4	2222.8	2.99	0.246
W	Budget Y1 expressed as J m ⁻² × 10 ⁻³	0.546	<u>0.560</u>	2.486	2.218	1.671	2.99	0.246

* All budgets use field estimates of P and A/C = 0.892.

† Field estimates are in italics and laboratory derived estimates are underlined.

In block Y of Table 3 field estimates of both P and C were used to calculate energy budgets for the whole population (Y1). Assimilation was calculated from C times the assimilation efficiency (0.892) and $Ra = A - P$; Rr was calculated as for budget Z1. Budget Y1 indicates that population metabolism in the field was greater than minimum laboratory metabolism by a factor (Ra/Rr) of 3.79 compared with 2.54 in budget Z5.

Budgets are also presented for an individual female and for the model population mentioned above assuming all individuals were released from the egg sac at the time of peak reproduction (24 February). In Y2 the female was assumed to grow to maturity in average time and have average reproduction. The calculation was based on monthly estimates of P and field estimates of C . A three point floating average was used to estimate C for the period in which the spider would have passed through each size class and gave $P/A = 0.217$. In Y3 this individual budget was applied to the model estimates of the number of spiders passing through each size class to give a population budget and gave $P/A = 0.203$.

As mentioned earlier the calibration curve used to estimate field C was not tested below 10 °C but the mean spider temperature in the field was below this temperature between June and August 1972. The estimates of C for this period which were used in budgets Y1–3 are questionable and were higher than expected from the winter growth rates. Accordingly a further budget (X) was derived in which the factor Ra/Rr was assumed to remain constant between summer and winter. The budget for the summer months (Table 4) was calculated in the same manner used for budget Y1 using field estimates of P and C and deriving the other values. The value of Rr for the winter months was calculated as usual and multiplied by the factor Ra/Rr found for the summer month (2.986) to give Ra in winter. This was added to the winter P derived in the field to give A , and C derived as in budget Z1. The winter and summer budgets were added to give the annual budget (X) in which $P/A = 0.246$.

TABLE 4. Calculation of budget X (Table 3) described in the text*; units in $J \times 10^{-3}$

	Summer	Winter	Annual
P	<i>693.1</i>	<i>33.53</i>	<i>726.6</i>
C	<u>2967.3</u>	<u>339.2</u>	<u>3306.5</u>
A	2646.8	302.5	2949.4
Ra	1953.8	269.0	2222.8
Rr	<u>654.2</u>	<u>90.09</u>	<u>744.3</u>
Ra/Rr	2.986	2.986	2.986
P/A	0.262	0.111	0.246

* Field estimates are in italics and laboratory derived estimates are underlined.

Two factors have a major effect on the ratio Ra/Rr , namely feeding and temperature cycles. Feeding would be lower in winter, tending to reduce the factor, while the diurnal temperature range was greater in winter (Humphreys 1978) and would increase the factor; these will be discussed later.

DISCUSSION

The energy budgets

For the entire population the ratio P/A varied between 0.203 and 0.494 according to the method of calculation used, the ratio Ra/Rr being as great as 4.0. Considering firstly the

budgets presented in block Z of Table 3, R was estimated by various extrapolations from the laboratory but which accounted for the high field temperatures of the spiders caused by their behavioural thermoregulation. The budgets Z1–3 have high P/A ratios as would be expected from budgets in which R was calculated from resting respiration rates. In the laboratory respiration was increased 1.88 times following feeding whether measured in respirometers or by laboratory energy budgets (Humphreys 1977a, b). In the field there would be an additional respiratory cost of unknown magnitude associated with prey capture and thermoregulatory behaviour that was not adequately accounted for in laboratory energy budgets; budgets Z4 would tend to be a low estimate.

The effect on respiration of cycling temperatures which was included in budget Z5 is more difficult to interpret. Its reality and magnitude has been supported by various evidence and attributed to the effect of metabolic rate compensation (Humphreys 1975b, 1977a, b). Supported by evidence from the literature (Tribe & Bowler 1968; Anderson 1970) it has been argued that the magnitude of the effect is directly related to the range of the temperature cycle above the mean temperature. Respiration in the field should be greater than $1.35Rr$ found in the laboratory because: (i) mean daily spider temperatures in the field were mostly below that used in the laboratory cycling temperature experiments ($20\text{ }^{\circ}\text{C}$); (ii) the spiders thermoregulated during sunny periods at temperatures ($35\text{ }^{\circ}\text{C}$) higher than the maximum temperature used in the laboratory ($29.3\text{ }^{\circ}\text{C}$). Both factors would increase respiration and the effect of the first would be greater in winter as mean spider temperatures were further from the temperature at which they thermoregulated. The magnitude of the second can be estimated as $1.625Rr$ compared with $1.35Rr$ found in the laboratory experiments (see Humphreys 1973, pp. 263–6). This is cumulative with the effect of feeding ($1.88Rr$) giving $Ra/Rr = 3.06$. As the effects of (i) above and of field activity have not been included it is probable that respiration of *Geolycosa godeffroyi* in the field is greater than $3.06Rr$. This compares with a range in Ra/Rr for budgets calculated from field estimates of both P and C between 3.0 and 4.0 ($P/A = 0.20 - 0.25$) depending on the method of calculation.

The use of a synchronous release time for the population and the model population structure had little effect on P/A which varied between 0.20 and 0.22 and the greatest variation was found when winter Ra was estimated indirectly from the summer ratio of Ra/Rr in budget X giving $P/A = 0.25$. Budget Y1 would overestimate Ra due to the effect of low temperatures on the estimate of C in winter. The absolute energy budget for *G. godeffroyi* cannot be determined but should lie between budget Z5 and X being probably closer to the latter. In further discussion budget X is considered unless specified, with Ra/Rr and P/A being 2.99 and 0.246 respectively.

Comparison with other spider energy budgets

A number of partial or complete energy budgets is available for comparison with those derived for *G. godeffroyi*. The ratio of P/C in the web-building species *Araneus cornutus* Clerck was 0.17 and 0.13 in 2 successive years and in the same years the ratio for *A. quadratus* Clerck was 0.38 and 0.28 (Kajak 1967). These ratios compare with a variation in the estimates for *Geolycosa godeffroyi* of from 0.18 to 0.22. Kajak's estimates were derived from measurements of field growth rates and food caught in the webs. She assumed (Kajak 1967, p. 811) that the food caught in the webs equalled consumption, although she appreciated that all the food caught was not consumed (Kajak 1967, p. 809).

For the lycosids in a grassland ecosystem, P/C was 0.33 but only after the laboratory derived respiration rate had been increased by a factor of 3.57 to account for field activity

(Van Hook 1971). There was no indication whether this study considered reproduction and if not, the ratio would be considerably changed.

Edgar (1971) approached the energetics problem by ignoring formal respirometry. He examined a field population of *Pardosa lugubris* (Walckenaer) and determined the food consumption for each instar in the laboratory under growth rates similar to those found in the field. He estimated R by balancing the budget, having assumed that the ratio A/C was equal to 1.0 because of the difficulty of estimating FU , even in the laboratory; this assumption would have exaggerated his estimates of respiration. He estimated the ratios of $P/C=0.26$ and $P/R=0.37$, compared with the estimates for *Geolycosa godeffroyi* of 0.18–0.22 and 0.24–0.32 respectively. Edgar further estimated that 25.2% of P went into egg production compared with an estimated 25.3% in *G. godeffroyi*.

On a dry weight basis, a population of *Tarentula kochi* Keyserling had a ratio P/C of 0.21 but no further estimates were made (Hagstrum 1970a). Moulder & Reichle (1972) measured the standing crop of the spider population on a forest floor and obtained estimates of food consumption from radionuclide mass balance equations in a fully labelled ecosystem. Their data indicated that spiders within the size range of *Geolycosa godeffroyi* went into negative production at temperatures greater than 18 °C and an annual ratio P/A of 0.22. The latter two studies are the most comparable with the present work as some estimate of food consumption was obtained but they differ greatly in detail, approach and knowledge of the breeding biology and microenvironmental relations of the spiders; the various comparisons are summarized in Table 5.

The studies considered above approached the problems of energetics estimates for lycosids in diverse ways and with very different levels of sophistication and detail. Despite this, there is gratifying agreement between the final estimates, giving ratios of R/A from 0.71 to 0.80, except for that of Van Hook (1971). The latter was not primarily a study of lycosids and its broad scope necessarily resulted in a sparse knowledge of the spiders' biology. The estimate he obtained for population R/A of 0.63 was lower than the ratio of 0.68 he derived from laboratory feeding experiments and the power function in his regression model relating respiration to body weight was usually high (1.236) compared with other studies (see Humphreys 1977b).

Spiders belong to trophic levels three and four in which Kozłowski (1968) considered that the ratio of R/A would be about 0.6 for the whole trophic level. This ratio is certainly not applicable to lycosids, in which the estimated efficiencies are between 17 and 33% greater (Table 5). The range in the ratio R/A estimated for carnivorous invertebrates (Menhinick 1967) includes the range of estimates for lycosids.

The similarity between the energy relations of *G. godeffroyi* and those obtained for other lycosids, lends support to the validity of the estimates derived here and this attempt to determine the relevance of laboratory respirometry to field energetics. Arguments have been presented, many supported by experimental evidence, concerning the nature and causes of the increased respiration in the field. Provided that the relevant field microenvironment is known, and respirometry conducted in sufficient detail to assess its influence on respiration, reasonably reliable estimates of field respiration are possible. Failure to take account of these variables can lead to considerable errors in the estimates of field respiration.

Energy flow as a descriptive function

While population processes and interactions may conveniently be summarized in terms of an energy budget, the latter does not adequately represent many of the population

TABLE 5. Selected efficiencies from the energy budget of *Geolycosa godeffroyi* compared with those derived for other carnivores

Species or group	A/C	P/A	R/A	E/P	$\Delta B/P$	E/C	P/B	Authority
<i>Geolycosa godeffroyi</i>	0.892	0.205	0.795	1.055	-0.055	0.193	2.557	This study
Spider population	0.940	0.218	0.782					Moulder & Reichle 1972
<i>Pardosa lugubris</i>	1.00	0.264	0.711				1.70	Edgar 1971
<i>Pardosa patustris</i> (L).	0.819	0.356	0.644				0.443	Steigen 1975
<i>Tarentula kochi</i> *		0.236	0.756					Hagstrum 1970a
<i>Lycosa</i> spp.	0.905	0.369	0.627	1.00				Van Hook 1971
<i>L. rabida</i> Walckenaer	0.908	0.32	0.68					Van Hook & Moulder 1969
(laboratory)								
<i>Urodacus vashenkoi</i> (Birula)	0.924	0.370	0.630	0.518	0.482	0.177	0.86	Shorthouse 1971
(Scorpionidae)								
Oribatei (Acarida)	0.201	0.214	0.786					Engelmann 1961
<i>Pyrrhosoma nymphula</i> (Sulzer)	0.899	0.518	0.417			0.08-0.30		Lawton 1971
(Zygotera, larvae)	0.884	0.475	0.485			0.340	4.26	Lawton 1971
Carnivorous invertebrates		0.105-0.375	0.625-0.895			0.183	2.53	Menimick 1967
Trophic level 1	0.02	0.62	0.38	0.18		0.02		Kozłowski 1968
2	0.82	0.42	0.58	0.27		0.13		
3	0.90	0.40	0.60	0.23		0.18		
4	0.99	0.37	0.63	0.04		0.02		

* Dry weight basis.

characteristics and may not be considered as an ecological Rosetta Stone. Population characteristics may be expressed in different units, none of which are intrinsically more informative than the others. The disparity between the various methods of representing the population characteristics of *G. godeffroyi* is shown in Fig. 1, where the various factors are expressed as a percentage distribution between the various size classes.

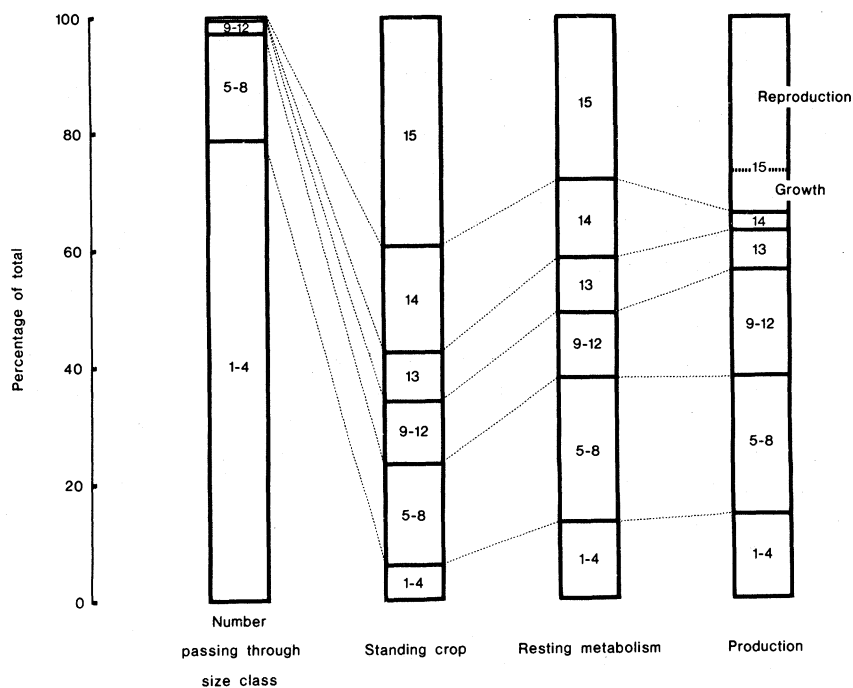


FIG. 1. Various population parameters for *Geolycosa godeffroyi* partitioned amongst the various size classes as a percentage of the total estimate.

Size classes 1 to 8 represented 97% of the estimated number of spiders passing through the size classes but only 23.4% of the standing crop and about 38% of both production and respiration. The increase in respiration over the standing crop is accounted for by the greater weight specific respiration of the smaller size classes. This difference is emphasized in *G. godeffroyi* due to the great size differential between the largest and smallest spiders. Size class 15 spiders accounted for only 0.1% of the estimated number of spiders passing through all size classes but for 39% of the standing crop and 28% of the respiration. The standing crop and respiration of size classes 14 and 15 were inflated by the long period during which these size classes were present in the population.

Relationship to other studies

One aim of science is to derive simplifying predictive models; in ecological energetics community analysis would be simplified if species could be grouped in some way (e.g. short versus long lived, aquatic versus terrestrial, or to trophic types) according to characteristic energetic efficiencies. It is a prime function of single species studies to provide a framework on which such generalization may be built. In the following paragraphs I want to consider some of the generalizations that have been proposed.

Kozłowski (1968) examined the various efficiencies derived from a series of five ecosystem studies and concluded that there were trends in the efficiencies related to trophic level. While they do not stand up to statistical analysis there are consistent trends within these studies and by their nature there was considerable room for error. If Kozłowski's conclusions are correct it should be possible, from the large number of studies available, to arrange the ratio P/R , or a derivative of it, so that there would be a clustering in the data related to trophic level.

Engelmann (1966) suggested that in animal populations there was a linear relationship between annual P and R per unit area. Golley (1968) and Hughes (1970) added further data to the relationship but did not re-analyse it. The suggestion was first seriously examined by McNeill & Lawton (1970) who compiled the considerable body of data then available. Plotting $\log P$ against $\log R$ they were able to separate the homoiotherms from the poikilotherms. They considered that when enough data were available for the long-lived poikilotherms they would be separable from the short-lived poikilotherms due to the former's increased respiratory cost while overwintering. Shorthouse (1971) added data from a further twenty poikilothermic species (Menhinick 1967; Shorthouse 1971; Van Hook 1971) to those analysed by McNeill & Lawton but excluded the data of Wignarajah (1968) and Lawton (1971) as they were sufficiently off-line to have undue effect on the relationship. By separating aquatic from terrestrial species he derived the relationships in Table 6 which had narrower confidence intervals than those obtained by McNeill & Lawton (1970) in which no distinction was made as to habitat. The aquatic species had a higher respiratory cost than terrestrial species but Shorthouse pointed out that the aquatic grouping also contained most of the long lived species and that many were detritivores.

TABLE 6. Equations relating annual population production (P) to respiration (R) for aquatic and terrestrial poikilotherms (from Shorthouse 1971; units are kcal m^{-2})

	Equation	95% prediction intervals
Terrestrial	$\log R = 0.9216 \log P + 0.2583$	$R = -2 \pm 0.6538$ $R = 3.0 \pm 0.7239$
	$\log P = 0.9929 \log R - 0.3074$	$P = -2 \pm 0.6867$ $P = 3.0 \pm 0.7434$
Aquatic	$\log R = 0.6437 \log P + 1.1807\dagger$	$R = 0 \pm 0.6471$ $R = 3.0 \pm 0.6463$
	$\log P = 1.149 \log R - 0.9651$	$P = 0 \pm 1.0749$ $P = 3.0 \pm 0.8254$

* Slope different from 1.0 ($0.01 > P > 0.001$)

The 'Engelmann line' relationships derived by McNeill & Lawton (1970) are important for it led them to propose that there was an inverse relationship between the net population production efficiency (P/A) in the short-lived poikilotherms and their annual production. Furthermore, the relationships that they derived are currently being used to estimate population production from laboratory derived respiration data (Phillipson 1971b; Mason 1971, 1977).

There can be no doubt that the general form of the relationship in the Engelmann line is correct or that the separation of the homoiotherms from the poikilotherms is valid. If Kozłowski's proposals are valid, it should be possible to separate the trophic levels within

a McNeill and Lawton type of analysis, but this is not the case. An examination of the data included in the analyses of McNeill & Lawton (1970) also raises questions about the validity of attempts to make the fine divisions within the poikilotherm data that have been proposed.

It is widely accepted that the determination of R by the extrapolation of laboratory respiration data may incur serious errors (Phillipson 1963, 1970; Odum, Connel & Davenport 1962; Mann 1965, 1969; Warren & Davis 1967). This acceptance is further shown by the propensity for adjustments to be made to such data to correct them for 'field activity'. The recommendation that respiration in fish should be increased by a factor of 2.0 to account for field activity (Winberg 1956) has been applied to other groups without justification (e.g. Saito 1967; Sameoto 1972). On the other hand, the maintenance costs of fish in streams may be less than those in aquaria because the random activity of the fish in the latter may be equal to, or greater than, the activity required to maintain station in a stream (Warren & Davis 1967, p. 200).

Considering the data included in McNeill & Lawton (1970) and Shorthouse (1971), it is appropriate to examine how R was estimated. I will exclude from consideration studies which concern only part of the life history of the species. In most of the studies considered, P was estimated in the field and R was estimated by the extrapolation of some laboratory determined level of respiration. The methods used in the respirometry varied considerably. In a number of the studies, no information was given about the thermal history or the nutritional state of the experimental animals (Odum & Smalley 1959; Smalley 1960; Wiegert 1964; Healey 1967; McNeill 1971). It has been shown in this study and elsewhere, that the definition of these conditions can considerably influence the interpretation placed on the estimates.

Of those studies in which the experimental conditions were defined, in some animals were used after a period of starvation and tested at the adaptation temperature (Kuenzler 1961), or over a range of temperatures from one preconditioning temperature (Shorthouse 1971). The former approach is similar to my determination of resting metabolic rate. Van Hook (1971) determined resting metabolic rate and increased it by the equivalent of my factor R_a/R_r determined from feeding experiments. Mann (1965) measured post-absorptive respiration while the fish were swimming at a constant speed. His results mainly account for the separation of the aquatic from the terrestrial species found by Shorthouse (1971) and of the long from short lived poikilotherms by McNeill & Lawton (1970).

In a further group of studies, the respiration of aquatic species was measured in respirometers in the field immediately after removal of the animals from the water, and at the habitat temperature (Teal 1957; Tilley 1968). This method is probably the most reliable for it maintains the animals close to their natural conditions and would, if conducted frequently enough, reflect changes in the nutritional state, thermal history and breeding condition of the animals.

A number of workers estimated R , both from the extrapolation of laboratory respiration data and from estimates obtained by measuring P , and C or FU in the field (Odum, Connel & Davenport 1962; Engelmann 1961; Hughes 1970; Lawton 1971). In the first work cited, laboratory derived estimates of R for an orthopteran had to be increased by 2.9 times to bring them to the level obtained from the field derived estimates but Hughes (1970) and Lawton (1971) found close agreement between the laboratory and field derived estimates of R for the bivalve *Scrobicularia plana* (Da Costa) and the larvae of *Pyrrhosoma nymphula* (Sulzer) respectively. Avery (1971, and personal communication) found

close agreement between four independent methods, including respiration measurements, of estimating the daily food requirements of the lizard *Lacerta vivipara* Jacquin.

In addition, various procedures have been used to correct laboratory derived estimates of R to the field temperatures; they range from no adjustment to detailed corrections based on a knowledge of the microenvironment of the species and its movement (Shorthouse 1971). Failure to consider temperature other than ambient air temperature may lead to errors in the estimation of R as high as 52% even if the appropriate measure of respiration has been made (Humphreys 1977b).

Corrections for temperature would generally have been more accurate for aquatic than for terrestrial species because large temperature changes in water tend to be seasonal rather than daily. In addition, there is less possibility of an aquatic species selecting a microenvironment that departs widely from the thermal conditions of the general water mass (but see Cameron, Kostoris & Penhale 1973). Aquatic species can be maintained in respirometers under conditions which are similar to their normal habitat, while the conditions to which terrestrial species are exposed may be difficult to determine. These factors are likely to have made the estimates of R for aquatic species more reliable than those obtained for terrestrial species.

Any attempt to draw conclusions of a more general nature from single species studies should take into account the methods used to estimate R . While numerous methods have been employed, they can be grouped into several categories based on a subjective assessment of the level of R likely to be measured. In this classification it is assumed that the true value of R was most closely approximated in those studies which estimated R from field estimates of P and either C or FU , or from long term feeding experiments. Estimates based on respiration of active animals, that is animals showing sustained locomotion in the respirometer, are assumed to give the highest estimate of R and those based on estimates extrapolated from some other laboratory measure of respiration the lowest estimates of R . Estimates from aquatic species are assumed to be more reliable than those for terrestrial species for the reasons discussed above.

In Table 7, the ratio of annual population respiration to production for a number of species is set out. Some of the data used by McNeill & Lawton (1970) have not been included because they do not cover the complete life cycle. I have also included more recent data and they are plotted in Fig. 2 ranked according to the classification set out above. Each of the three classes has been divided into aquatic and terrestrial species. The data in column 3 have been further subdivided into those terrestrial species which belong to taxa in which some members are known to thermoregulate and in which there was the possibility of a major error in temperature correction. These include lycosids and Orthoptera (column 3c) and perhaps could include some leaf dwelling species due to the large temperature excess of leaf surfaces (Burrage 1971; Ehrler 1975; Lange *et al.* 1975; Patten & Smith 1975).

There is disturbing agreement between the trend of the data in Fig. 2 and the prior subjective assessment of the possible bias introduced by the method used to estimate R . The situation is not as clear as it could be, due to the distribution of trophic types within the analysis. Herbivores predominate in the right hand part of Fig. 2 and carnivores in the left. According to Kozlowski (1968) the former would be expected to have a lower R/P ratio than the latter. Nevertheless, all the species in which R was estimated by methods other than the extrapolation of respirometry on inactive animals, have a R/P ratio greater than 2.5, irrespective of their food type. Of estimates for terrestrial species which relied in the respirometry of inactive animals (columns 3b and 3c), 89% have R/P ratios less than

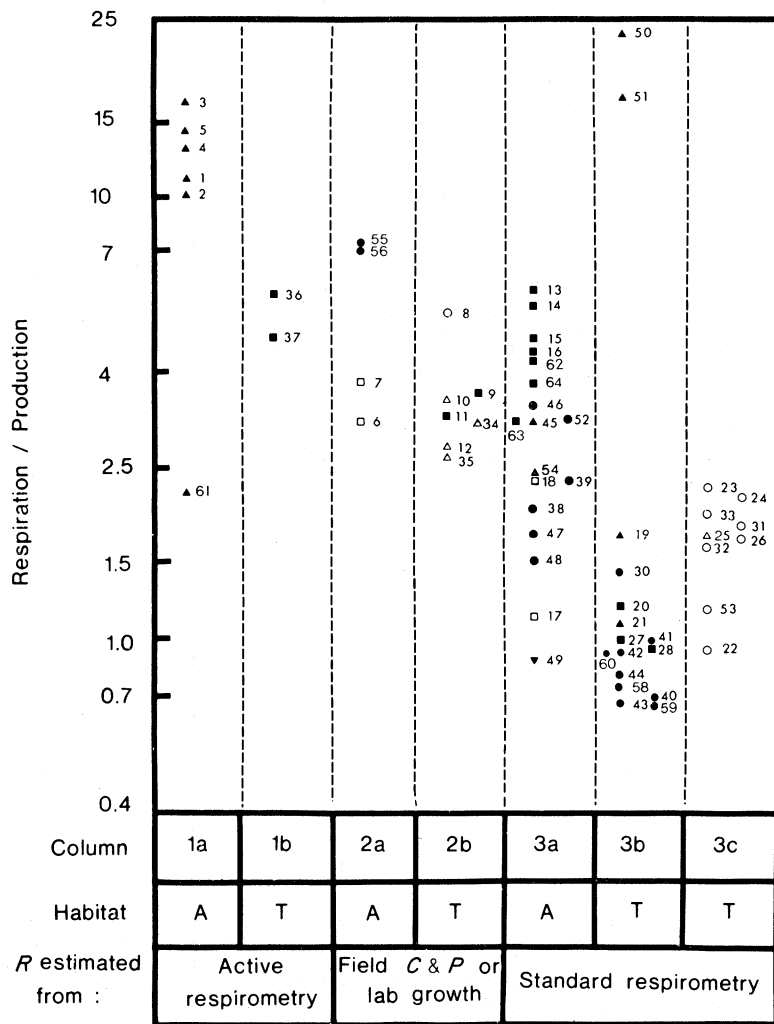


FIG. 2. Data from Table 7 grouped according to the method used to estimate *R*. The numbers at each point correspond to the numbers in the first column of Table 7. A, aquatic; T, terrestrial: \blacktriangle , carnivore (\triangle , araneae); \blacksquare , detritivore (\square , lamellibranchiata); \bullet , herbivore (\circ , orthoptera); \blacktriangledown , omnivore. Numbers 29 and 57 are not plotted as they fall outside the limits of the graph. Data are considered only from studies in which production was estimated in the field and which included the entire life cycle. The compilation is not otherwise selective nor is it exhaustive.

2.5, whatever their trophic type. Some of these latter points had already been adjusted upwards to account for field activity; for example, the points numbers 22–25 in column 3c represents the data from Van Hook (1971), in which *R* had been adjusted upwards by between 1.85 and 3.57 times.

Of particular significance are the points derived for the same or similar taxa by the different methods. These fall into three groups; the Lamellibranchs (Nos 6, 7, 17 and 18 in Fig. 2), the Orthoptera (Nos 8, 22, 23, 24, 26, 31, 32 and 33) and the Araneae (Nos 10, 12, 25, 34 and 35). Budgets derived from methods in column 2 ('field methods') gave *R/P* ratios greater by a factor of 2.0 than those derived using laboratory respirometry

TABLE 7. Respiration/Production in populations of ectothermic animals

Number in Fig. 2	Genus or family	Group or English name	Terrestrial (T) or Aquatic (A)	Trophic level			R/P	Reference
				Detritivore (D)	Herbivore (H)	Carnivore (C)		
1	<i>Rutilus</i>	Roach	A		C		11.07	Mann 1965
2	<i>Alburnus</i>	Bleak	A		C		10.30	Mann 1965
3	<i>Leucisus</i>	Dace	A		C		12.89	Mann 1965
4	<i>Perca</i>	Perch	A		C		12.89	Mann 1965
5	<i>Gobio</i>	Gudgeon	A		C		14.23	Mann 1965
6	<i>Scrobicularia</i>	Lamellibranchiata	A		D		3.12	Hughes 1970
7	<i>Scrobicularia</i>	Lamellibranchiata	A		D		3.84	Hughes 1970
8	3 Orthoptera	Orthoptera	T		H		5.40	Odum, Connel & Davenport 1962
9	Oribatid mites	Acari	T		D		3.67	Engelmann 1961
10	All spiders	Araneae	T		C		3.58	Moulder & Reichle 1972
11	<i>Oniscus</i>	Isopoda	T		D		3.21	Phillipson 1967
12	<i>Paradosa</i>	Lycosidae	T		C		2.70	Edgar 1971
13	<i>Littorina</i>	Gastropoda	A		D		6.14	Odum & Smalley 1959
14	<i>Gammarus</i>	Amphipoda	A		D		5.68	Tilley 1968
15	<i>Limnodrilus</i>	Tubificidae	A		D		3.01	Teal 1957
16	<i>Asellus</i>	Isopoda	A		D		4.49	Teal 1957
17	<i>Pisidium</i>	Lamellibranchiata	A		D		1.11	Teal 1957
18	<i>Scrobicularia</i>	Lamellibranchiata	A		D		2.34	Kuenzler 1961
19	<i>Urodacus</i>	Scorpionidae	T		C		1.70	Shorthouse 1971
20	<i>Onychiurus</i>	Collembola	T		D		1.17	Healey 1967
21	<i>Nebria</i>	Carabidae	T		C		1.07	Manga 1972
22	<i>Melanoplus</i>	Orthoptera	T		H		0.94	Van Hook 1971
23	<i>Conocephalus</i>	Orthoptera	T		H		2.19	Van Hook 1971
24	<i>Pteronemobius</i>	Orthoptera	T		H		2.11	Van Hook 1971
25	<i>Lycosa</i>	Lycosidae	T		C		1.70	Van Hook 1971
26	<i>Orchelimum</i>	Orthoptera	T		H		1.72	Smalley 1960
27	<i>Japonaria</i>	Diplopoda	T		D		1.15	Saito 1967
28	<i>Japonaria</i>	Diplopoda	T		D		1.00	Saito 1967
29	<i>Pogonomyrmex</i>	Formicoidea	T		H		> 155.6	Golley & Gentry 1964
30	<i>Philaenus</i>	Hemiptera	T		H		1.42	Wiegert 1964
31	<i>Melanoplus</i>	Orthoptera	T		H		1.76	Wiegert 1965
32	<i>Melanoplus</i>	Orthoptera	T		H		1.60	Wiegert 1965
33	<i>Melanoplus</i>	Orthoptera	T		H		1.90	Wiegert 1965
34	<i>Geolycosa</i>	Lycosidae	T		C		3.10	Humphreys 1973
35*	<i>Tarentula</i>	Lycosidae	T		C		2.58	Hagstrum 1970a

36	<i>Cognetha</i>	Enchytraeidae	T	D	6-10	Standen 1973
37	<i>Cognetha</i>	Enchytraeidae	T	D	2-81	Standen 1973
38	<i>Diaptomus</i>	Copepoda	A	H	1-98	Kibby 1971
39	<i>Diaptomus</i>	Copepoda	A	H	2-35	Kibby 1971
40	<i>Leptoterna</i>	Hemiptera	T	H	0-72	McNeill 1971
41	<i>Leptoterna</i>	Hemiptera	T	H	0-96	McNeill 1971
42	<i>Leptoterna</i>	Hemiptera	T	H	0-92	McNeill 1971
43	<i>Leptoterna</i>	Hemiptera	T	H	0-71	McNeill 1971
44	<i>Leptoterna</i>	Hemiptera	T	H	0-82	McNeill 1971
45	<i>Hedriodiscus</i>	Diptera	A	H	3-05	Stockner 1971
46	<i>Hedriodiscus</i>	Diptera	A	H	3-37	Stockner 1971
47	<i>Hedriodiscus</i>	Diptera	A	H	1-07	Stockner 1971
48	<i>Hedriodiscus</i>	Diptera	A	H	1-45	Stockner 1971
49	<i>Cherax</i>	Decapoda	A	O	0-84	Woodland 1967
50	<i>Lithobius</i>	Chilopoda	T	C	23-5	Wignarajah 1968
51	<i>Lithobius</i>	Chilopoda	T	C	17-1	Wignarajah 1968
52	<i>Strongylocentrotus</i>	Echinoidea	A	H	2-57	Miller & Mann 1973
53	<i>Encopitoloophus</i>	Orthoptera	T	H	1-26	Bailey & Reigert 1973
54	<i>Pungitius</i>	Stickleback	A	C	2-42	Cameron, Kostoris & Penhale 1973
55	<i>Ancyclus</i>	Gastropoda	A	H	7-93	Streit 1976
56	<i>Ancyclus</i>	Gastropoda	A	H	7-47	Streit 1976
57	<i>Neanthes</i>	Polychaeta	A	C	0-368	Kay & Brafield 1973
58	<i>Eucallipterus</i>	Aphididae	T	H	0-725	Llewellyn 1972
59	<i>Eucallipterus</i>	Aphididae	T	H	0-683	Llewellyn 1972
60	<i>Rhynchaenus</i>	Curculionidae	T	H	0-913	Grimm 1973
61	<i>Metamysidopsis</i>	Mysidacea	A	C	2-13	Clutter & Theilacker 1971
62	<i>Ferrissia</i>	Gastropoda	A	D	4-26	Burky 1971
63	<i>Hyalella</i>	Amphipoda	A	D	2-99	Mathias 1971
64	<i>Crangonyx</i>	Amphipoda	A	D	3-79	Mathias 1971

* Based on dry weight.

($F_{1,16} = 28.9$, $P < 0.001$); interestingly this factor is the same as that suggested by Winberg (1956) to correct fish respiration data to field conditions.

To take the specific case of *Geolycosa godeffroyi* (Fig. 2; No. 34 in column 2b) the R/P ratio falls amongst the cluster of points obtained for spiders by various authors. The lowest laboratory derived budget (Z1) gave $R/P = 1.02$ but with additional experiments based on a knowledge of conditions in the field it was possible to increase this ratio to within the range of field derived measurements in which R/P lay between 3.1 and 4.2.

True assimilation figures are difficult to obtain so Macfadyen (1967) thought it adequate to use respiration data instead. Golley (1968) considered that the extrapolation of laboratory data to the field was not a serious problem while Phillipson (1967) speculated that respiration measurements made at the mean annual temperature of the animal's environment may suffice to describe respiration in the field. However this environment may be difficult to describe; for two terrestrial species, in which detailed activity and temperature data are available, respiration estimates were 20% and 52% greater than expected from the mean monthly air temperature for *Urodacus yashenkoi* Birula (data from Shorthouse 1971) and *Geolycosa godeffroyi* respectively (both derived in Humphreys 1977b).

Macfadyen (1967) stated that R/P greatly exceeded unity except in herbivorous insects. Phillipson (1973) calculated community budgets using $P/A = 0.43$ and 0.065 for invertebrate plant feeders and invertebrate carnivores ($R/P = 1.32$ and 14.4) respectively. Slobodkin (1959) thought that P/A could not exceed $0.25-0.30$ ($R/P = 2.3-3.0$) in steady state populations and agreed with Hutchens (1951) who predicted this on consideration of biochemical efficiency. Laboratory studies have shown a wide range in P/A from about 0.2 to 0.9 (Welch 1968, $R/P = 0.1$ to 4.0) but not all were steady state populations: young individuals have higher gross growth efficiencies (P/C) than older individuals (Phillipson 1966) so that expanding populations will be more efficient than stable age or declining populations.

If the levels of efficiency considered realistic by Hutchens and Slobodkin are correct, then values of R/P less than 2.5 would be unacceptable and exclude most of the studies in columns 3b and 3c of Fig. 2. It is widely accepted in the literature that the ratio R/A exceeds 0.8 (e.g. Hutchinson 1959; Engelmann 1968; Golley 1968) which gives a ratio of R/P of 4.0 or greater; few of the estimates in Fig. 2 are greater than this value. These inconsistencies between theoretical efficiencies, field and laboratory measurements, and the generalizations, clearly need considerable evaluation. In particular explanation is needed of the mechanisms by which herbivorous insects can obtain such great efficiency.

Wiegert (1968) discussed the theoretical and practical errors involved in the calculation of energy budgets and thought it sufficient at the time to qualify accordingly any conclusions based on energy budgets. The errors he considered were all small and, despite their important implications, have little relevance to most field studies in which the potential errors involved in the estimation of R alone are an order of magnitude greater.

I have not considered the estimation of P which is routinely measured in the field and which has its own set of errors and potential bias. I have excluded it because it is more difficult to assess from published reports the level of accuracy and the direction of potential bias involved. I am left with the feeling that the resolution obtained (and perhaps obtainable) in many energy budgets is rather low; this has particular implications to those bold studies attempting to test hypotheses using energetics methodology such as the work of Sutherland (1972). If the general trends suggested in my analysis are real, namely that metabolic heat loss may have been underestimated frequently, then we

cannot 'accept field estimates at their face value in the hope that there is no consistent trend to the error introduced' (Slobodkin 1962).

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