

RESPIRATION STUDIES ON *GEOLYCOSA GODEFFROYI* (ARANEAE:LYCOSIDAE) AND THEIR RELATIONSHIP TO FIELD ESTIMATES OF METABOLIC HEAT LOSS

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Abstract—1. The respiration rate of *Geolycosa godeffroyi* shows a diurnal rhythm which drifts under constant conditions.

2. The values for the weight exponent b of the regression lines relating log respiration to log body weight varies from 0.793 to 0.847 within the temperature range 4–40°C.

3. Q_{10} values decreased with increasing temperature throughout the range tested (4–40°C) from about 2.3 to 1.5.

4. Activity (locomotion) and feeding increased the respiration rate above the resting level but neither the sex nor reproductive condition influenced the respiration rate.

5. A model is presented relating the resting metabolic rate of *G. godeffroyi* to live body weight, temperature and season. This model is applicable to a wide range of lycosid species.

6. The data are discussed in relation to respiratory physiology and with respect to field extrapolations of respiration data.

INTRODUCTION

Studies of the energy relations of populations in the field normally require the extrapolation of some laboratory data to supplement those derived from field studies. The most important laboratory measurement required is respiration which is normally added to a field estimate of production to give assimilation figures. However the respiration rates derived in the laboratory can be made to vary, according to the experimental conditions; in the case of fishes this variation may be through nearly two orders of magnitude (Weatherley, 1972). While it is widely accepted that extrapolating laboratory respiration figures to the field may incur serious error (Phillipson, 1963, 1970; Odum *et al.*, 1962; Mann, 1965, 1969; Warren & Davis, 1967) few respiration studies conducted for energetics work examine the problem seriously. Despite this adjustment factors are frequently applied to respiration data to account 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 indiscriminately to other ectotherm groups (e.g. Saito, 1967; Sameoto, 1972) often with little or no discussion.

Numerous methods have been used to obtain estimates of field oxygen requirements from laboratory respiration measurements. The use of starved or post absorptive animals to estimate the resting metabolic rate (RMR) has been commonly reported in the literature (e.g. Odum *et al.*, 1962; Shorthouse, 1971). If animals were readily available then the oxygen consumption may have been measured soon after collection and throughout the year (Phillipson, 1962; Stockner, 1971; Manga, 1972). This method takes into account life history and seasonal variation in the respiratory

rate. The rate/temperature (R–T) relationship is normally determined only once, with no check on the form of the R–T curve due to seasonal temperature compensation. RMR data have been used directly to estimate metabolic heat loss in the field (Hughes, 1970; Stockner, 1971) or with various adjustments to account for field activity. RMR measurements have been increased by a factor of two, as suggested by Winberg (1956), or up to 3.57 times, a factor indicated from laboratory feeding experiments (Van Hook, 1971). The validity of these various manipulations is difficult to determine but they were originally justified according to the manner in which the respiration measurements were made and from consideration of the biology of the species.

Variation in the estimates of metabolic heat loss with different food types is only about 5% with oxygen measurements, compared with about 10% from carbon dioxide measurements. In ecological work it is generally considered that no correction need be made for the food type (Petrušewicz & Macfadyen, 1970). In other than fasting animals, indirect measurements of metabolic heat production may be subject to as much as 10% error due to growth (Wiegert, 1968). Although these types of errors are large by physiological standards, they are small when compared with the probable errors involved in extrapolating laboratory data to estimate metabolic heat loss in the field, as will be shown here.

In this paper the respiration of the wolf spider *Geolycosa godeffroyi* (L. Koch) (Araneae: Lycosidae) is examined in the laboratory to determine the possible variation in respiration rates when the spiders are subjected to a series of biologically pertinent conditions.

MATERIALS AND METHODS

Geolycosa godeffroyi was collected from dry forest areas of the Australian Capital Territory. This species inhabits burrows for the most of its life and grows from 2.5 mg to up to 2700 mg over 2.5 years (Humphreys, 1976). The spiders maintain their body temperature in excess of air temperature throughout the day by basking in the sun and, at night, by withdrawing down their burrows and using the thermal lag in the soil temperature profile (Humphreys, 1974, 1975a).

Oxygen consumption was measured in electrolytic respirometers using saturated copper sulphate as the electrolyte. The electrolysis of copper sulphate solution may produce traces of ozone (Wager & Porter, 1961; Woodland, 1973); this way prevented from reaching the animal chamber by a barrier of soda lime (Belew, 1969) which also served to absorb carbon dioxide. The respirometers had interchangeable chambers so that the diameter could be changed to approximate the diameter of the burrows normally occupied by the spider under test; these conditions result in the spider remaining still in the chamber (Humphreys, 1973). The volume of the compensation chamber was adjusted to equal the volume of air in the animal chamber. Respirometers were maintained at the required temperature in a refrigerated incubator and each was connected in series with a direct current power supply and a volumetric coulometer maintained in a separate incubator at 30°C. Following an equilibration period measurements were made for 24 hr and the results corrected to standard temperature and pressure before analysis.

Experimental conditions

1. *Resting metabolic rate.* The spiders were adapted to the experimental conditions for from 7 to 10 days during which they were not fed. Experiments were conducted at 4, 10, 20, 30 and 40°C on spiders covering most of the size range found in the field.

2. *Effects of feeding.* Spiders were adapted in the same manner as for the resting metabolic rate experiments but were fed immediately before testing.

Spiders weighing more than 100 mg were tested individually in the respirometers but those <100 mg were tested severally. In the latter case spiders of similar size were used and separated to prevent interaction and cannibalism. Spiderlings from the back of the females were tested *en masse* as they were not cannibalistic at that stage.

RESULTS AND DISCUSSION

Periodicity

When hourly records were kept over several days on the oxygen consumption at 30°C a marked periodicity was often apparent similar to the results (Dresco-Derouet, 1961) obtained for a scorpion. The interval between the major peaks in oxygen consumption was 23.3 hr (S.E. = 1.4, n = 20). The peaks were not associated with a particular time of day. The periodicity recorded from spiders in laboratory actographs under constant conditions (20°C and continuous light) also drifted (Humphreys, 1973) and could account for the periodicity in the oxygen respirometry.

Anderson (1970) showed that *Lycosa lenta* Hentz had a pronounced diurnal rhythm in oxygen consumption, which decayed within 3 weeks under constant conditions; he did not determine at what point the rhythm was lost. He considered that the rhythm was accounted for by the normal activity patterns of the spider in the field. The data from *G. godeffroyi*

support his conjecture. He found similar rhythms in other hunting spiders but failed to find them in any of the web-builders he studied. Ulanoski & McDiffett (1972) studied diurnal variation in two mayfly nymphs and found a respiratory rhythm in *Isonychia* sp. but not in *Stenonema fuscum* and attributed this to differences in their behaviour. Circadian respiratory rhythms have been widely reported in arachnids (Phillipson, 1962; Hagstrum, 1970, Moulder & Reichle, 1972) and in other arthropods (Hebrant, 1970); failure to take them into account by conducting respirometry over short periods may lead to errors in the estimation of respiratory requirements.

The effect of sex on oxygen consumption

Males were only seasonally represented in the population (Humphreys, 1976) so there were sufficient data to examine the influence of sex on the oxygen consumption at only two temperatures. No significant differences were found in the rate of oxygen consumption between males and females at either 4°C ($t_{22} = 0.34$, n.s.) or 30°C ($t_{20} = 1.98$, n.s.). In further treatment of the results sex differences are ignored. Sex differences in respiration rates have not been reported for lycosids but males have greater respiration rates in both scorpions (Dresco-Derouet, 1964; Shorthouse, 1971) and carabid beetles (Manga, 1972).

The effect of weight on resting oxygen consumption

The results for all the RMR experiments are initially presented as regressions (log log) against the live weight of the spider (Fig. 1). All regression and correlation coefficients are significant at a probability of <0.001. The five sets of data show significant heterogeneity ($P < 0.001$) which is lost when the 30°C data are excluded ($0.1 > P > 0.05$). These lines are parallel ($P > 0.75$) but displaced ($P < 0.001$) when tested by an analysis of variance. The values for the slope vary from 0.795 to 0.847 with a mean slope of 0.821.

The mean slope for *G. godeffroyi* is different ($t_{256} = 2.66$: $0.01 > P > 0.001$) from the generalised mean slope of 0.756 ± 0.021 found by Hemmingsen (1960) but not from its upper limit ($t = 1.85$, n.s.). For arthropods generally the function lies between 0.70 and 0.85 (Scholander *et al.*, 1953; Edwards, 1946, 1958). Reichle (1968) determined this relationship for 10 species of forest floor arthropods and derived a slope of 0.84 ± 0.071 . Most of the determinations cited were measured between 15 and 25°C.

Some of the respiration data available on spiders are not comparable to those obtained for *G. godeffroyi* as they were expressed as a rate, with either no temperatures or no weight values presented (e.g. Breymer, 1967; Kajak, 1967). Many of the available data are compiled in Table 1 and compared with those obtained for *G. godeffroyi* at the same weight and temperature. Of the species in the cited works, *L. carolinensis* Walckenaer is the most comparable with *G. godeffroyi* as it grows to a similar size, is diurnally active and lives in burrows. The agreement between the various measurements is generally close.

Phillipson (1963) emphasised the dangers of using respiration measurements on an inter-specific basis, and Wood & Lawton (1973) showed that even intra-specific comparisons may be suspect if different popu-

lations were considered. The close agreement found in the RMR between various lycosid species, of diverse weights and under different temperature conditions, lends support for the establishment of a general model describing the RMR of lycosids. Such a model is presented later.

The effect of temperature on the resting metabolic rate

As with some other lycosids (Anderson, 1970) *Geolycosa godeffroyi* exhibits acclimation (Humphreys, 1975b) so it needs stressing that these data are derived from spiders adapted to the experimental conditions. The Q_{10} values can be calculated from the equations presented in Fig. 1; the statistics for these equations

have been presented elsewhere (Humphreys, 1975b) but the data have not been discussed. In general the Q_{10} dropped from about 2.3 in the 4–20°C range to about 1.5 in the 20–40°C range and was only slightly dependent on weight class.

In *G. godeffroyi* the Q_{10} (10–30°C) was 2.01, and a Q_{10} of 2.0 has frequently been considered as the norm for determinations of respiration within the active temperature range of ectotherms (Moulder & Reichle, 1972). Calculating from the data of Miyashita (1969) for *Lycosa T-insignita* Boes. et Str. the Q_{10} (15–20°C) = 2.54 and dropped to Q_{10} (25–30°C) = 1.84 as the temperature rose. From Hagstrum's (1970) data, the relationships for *Tarentula kochi* Keyserling

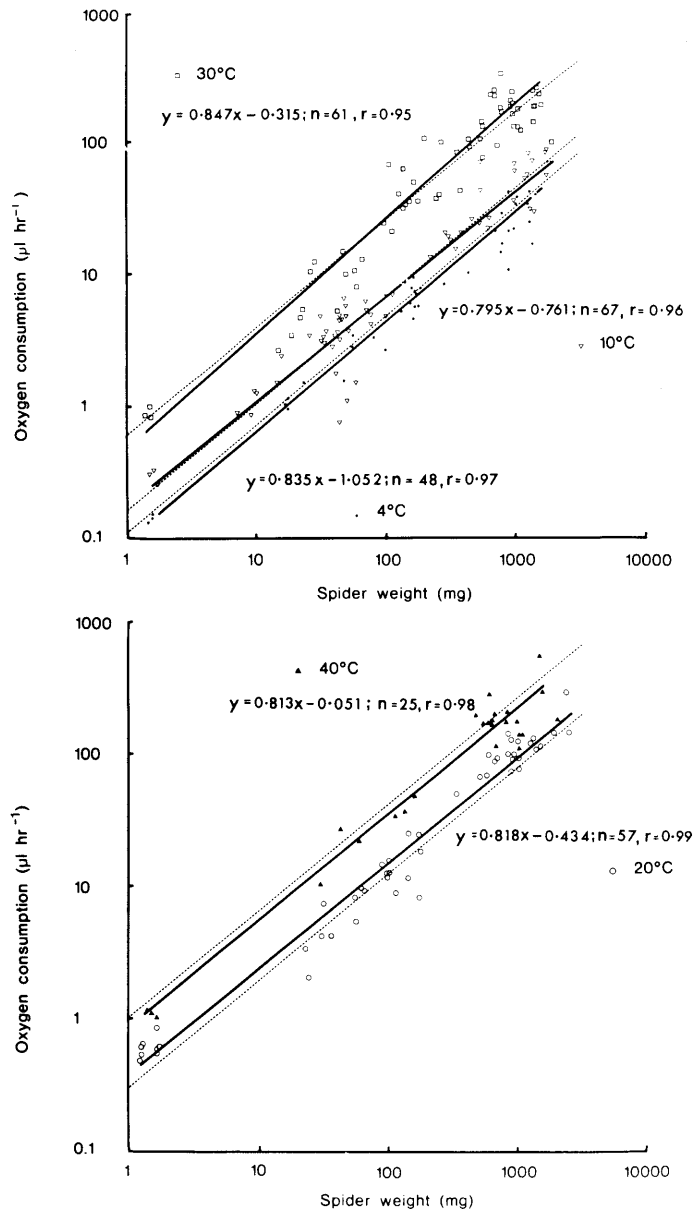


Fig. 1. The relationship between the live weight ($\log_{10} Y$) of *Geolycosa godeffroyi* and its resting oxygen consumption ($\log_{10} X$) at five temperatures. The solid lines are drawn from the appropriate regression equations given on the figure which take the form $Y = bX + a$, n = number in the sample and r = correlation coefficient. The broken lines show the fit of the multiple regression model derived from all the data (see text).

Table 1. Comparison of the respiration of *G. godeffroyi* with the values for lycosid spiders reported in the literature

Species	Temperature (°C)	Weight (mg)	Respiration at cited weight ($\mu\text{l O}_2 \text{ hr}^{-1}$)		Authority
			Cited species	<i>G. godeffroyi</i>	
<i>Lycosa pseudoannulata</i> *	29	100	29.87	23.94	Itô, 1964
<i>Lycosa lenta</i> (Hentz)	20	970	90.0	102.1	Anderson, 1970
<i>L. carolinensis</i> Walckenaer	39-41	1000	230.0	244.3	Moeur & Eriksen, 1972
<i>Lycosa</i> sp.	20	200	50†	28.1	Scholander <i>et al.</i> , 1953
<i>L. T-insignita</i> Boes et Str.*	20	60	10.66	10.48	Miyashita, 1969
<i>L. T-insignita</i> Boes et Str.	30	60	25.86	15.53	Miyashita, 1969
<i>L. rubida</i>	20	400	95†	49.5	Van Hook, 1971
<i>Tarentula kochi</i> Keyserling	20	100	17	15.92	Hagstrum, 1970
<i>Tarentula kochi</i> Keyserling	30	100	36	23.93	Hagstrum, 1970
<i>Schizocosa</i> sp.	20	23.4	5.87	4.85	Reichle, 1968
Lycosids	20	100	29†	15.92	Moulder & Reichle, 1972
Lycosids	20	1000	220†	104.70	Moulder & Reichle, 1972
<i>Pardosa laura</i> Karsch.	25	30	22.28	6.67	Nakamura, 1972
<i>Trochosa ruficola</i> (Degee)	20	120.6 (101.2)‡	32.83 (18.13)‡	18.56	Myrcha & Stejgwill-Laudańska, 1973
<i>Lycosa pullata</i> (Clerc.)	20	16.2 (9.0)	7.11 (1.53)	3.59	Myrcha & Stejgwill-Laudańska, 1973
<i>Pirata latitans</i> (Blackw.)	20	9.0 (9.0)	4.07 (4.67)	2.22	Myrcha & Stejgwill-Laudańska, 1973

* RQ. assumed to be 0.85.

† Approximate value read from graph.

‡ Figures in brackets represent values after 7 days without food and are thus comparable to the data from *G. godeffroyi*.

were Q_{10} (15–20°C) = 25.0 for the smallest and 6.1 for the largest juveniles and Q_{10} (20–30°C) = 6.9 for the smallest and 2.12 for the largest juveniles. Too few details were presented to assess the validity of these high Q_{10} values in *T. kochi* and they contrast with other determinations in the literature. The data for *L. lenta* (Anderson, 1970) gives Q_{10} (10–20°C) = 3.23 and Q_{10} (20–30°C) = 1.60 for spiders tested at the adaptation temperature. Moulder & Reichle (1972) reported Q_{10} values which did not differ from 2.0 over the range 15–25°C.

Moeur & Eriksen (1972) presented respiratory data for *L. carolinensis* at different times of the year and close to the upper lethal temperature. They showed a variation in Q_{10} from 0.15 near the upper lethal temperature to 4.21 just below this temperature. From their data the Q_{10} (29–39°C) = 1.8 in summer and fell to 1.26 in winter. The summer Q_{10} (23.5–33°C) was 1.35. These compare with determinations for a 1000-mg *G. godeffroyi* of Q_{10} (20–30°C) = 1.61 and Q_{10} (30–40°C) = 1.45, showing that the two species had similar metabolic responses to thermal changes over their upper temperature ranges. Moeur & Eriksen (1972) accounted for the seasonal changes in the Q_{10} by a lateral shift in the rate temperature (R–T) curve but their data are not conclusive.

While there are no data in the literature obtained near the lower temperatures used in the present experiments or covering such a wide size range, those available show that other lycosids have a response to thermal conditions similar in both magnitude and direction to *G. godeffroyi*, with the exception of the data from Hagstrum (1970). In general the Q_{10} in lycosids drops with increasing temperature.

Derivation of a model describing the resting metabolic rate

Multiple regression analysis was used to derive the relationship between the RMR of *G. godeffroyi*, the weight of the spider and temperature. The equation

has the form: $Y (\log_{10} \mu\text{l O}_2 \text{ hr}^{-1}) = -1.069 + 0.816 \pm 0.0128 (\log_{10} \text{ mg live wt}) + 0.028 \pm 0.0010 (^\circ\text{C})$, ($n = 258$, $F = 2488.6$, $P < 0.001$) and accounts for 95.1% of the variance; there is good agreement with the original regression lines (Fig. 1). The addition of month of year to the regression (as described in Humphreys, 1976, p. 67) was significant ($0.05 > P > 0.02$) giving: $Y (\log_{10} \mu\text{l O}_2 \text{ hr}^{-1}) = -1.003 + 0.813 \pm 0.0128 (\log_{10} \text{ mg live wt}) + 0.028 \pm 0.0097 (^\circ\text{C}) - 0.017 \pm 0.0075 (\text{month})$ ($n = 258$, $F = 1686.2$, $P < 0.001$, $r^2 = 0.953$). This apparent seasonal variation was not due to cross correlation as indicated by partial correlation ($P < 0.01$) to exclude the effect of weight. There was a seasonal variation in respiration of about 20%; respiration was greater in winter than in summer; this agrees in both magnitude and direction with other work. In *Lycosa carolinensis* there was an increase in summer over winter respiration of 28% in the temperature range 29–39°C (Moeur & Eriksen, 1972).

A similar model was presented for *L. rubida* Walckenaer by Van Hook (1971) and had the form $Y = 0.376X^{1.236} 0.0693(T-20)$ where $Y = \mu\text{l O}_2 (\text{mg hr}^{-1})$; $T = ^\circ\text{C}$ and $X = \text{body weight}$ (the unit was unspecified). Assuming X to be mg dry weight the model approximates the data he presented for 20°C. This model departs widely from the model presented for *G. godeffroyi* but the exponent to which the weight was raised was unusually high (1.236) in *L. rubida*. Van Hook (1971) claimed that this power function was similar to that found by Moulder (1969) of 1.37 for forest floor spiders but Moulder (1969 p. 48) emphasised that the power function he found was close to the expected value and found that it varied from 0.91 at 15°C to 0.6 at 25°C. There is no support in the literature for the high power function found by Van Hook and considering the small number (27) of respiration measurements used in his model and the small temperature range (15–25°C), no valid comparison can be made between his model and that obtained for *G. godeffroyi*.

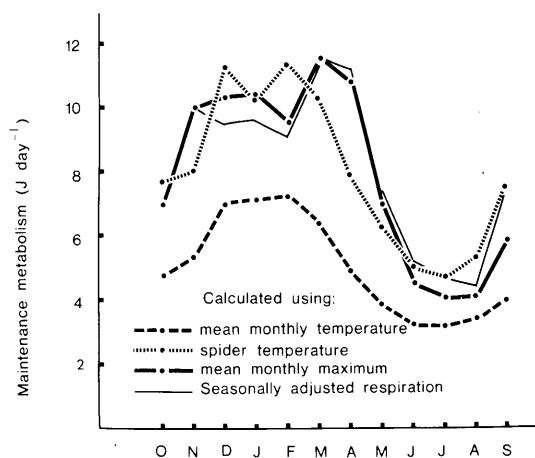


Fig. 2. Monthly metabolic heat loss from a 141 mg *Geolycosa godeffroyi* calculated using the model and various field temperature data.

The regression equation without seasonal weighting was used to calculate maintenance metabolism from the mean monthly and the mean monthly maximum screen temperatures and from the spider cephalothorax temperatures (Humphreys, 1974). The regression equation with seasonal weighting was used to calculate the seasonally adjusted respiration from the actual spider temperatures.

Use of the model

The temperature of spider cephalothoraces in the field was measured with implanted thermocouples and available for each 0.25 hr throughout 24 hr on 26 days spread throughout one year (Humphreys, 1973, 1974). The data are used to calculate the respiration of a size class 10 *G. godeffroyi* weighing 141 mg (Humphreys, 1976) throughout the year. This is calculated, both with and without seasonal adjustment. Calculations are also presented using the mean monthly temperature in the field, a measure often used in the extrapolation of laboratory data to the field, and the mean monthly maximum temperature (Fig. 2).

Without the seasonal adjustment the estimated resting metabolic heat loss (2912J) from the spiders was similar to that expected from the mean monthly maximum temperatures (2978J) rather than the mean monthly temperatures (1908J). Including the seasonal adjustment (2743J) reduced the summer heat loss slightly and increased the winter heat loss but the curve was still close to that expected from the mean monthly maximum temperatures. On an annual basis the metabolic heat loss of the seasonally unadjusted determinations was 97.8% of the seasonally adjusted loss. The seasonally adjusted estimate accounted for 92.1% of the estimate from the mean monthly maximum temperature and were respectively 152% and 144% greater than the metabolic heat loss estimated using the mean daily temperatures. In the case of *G. godeffroyi* the use of ambient air temperatures rather than actual body temperatures would seriously underestimate the resting metabolic heat loss in the field.

It may be argued that *G. godeffroyi* is a special case as it basks in the sun and that there is no cause for concern about the use of mean temperature values in the extrapolation of laboratory respiration data to

the field. The only comparative data available, in which the cost of maintenance metabolism was calculated in a similar manner, is that of Shorthouse (1971) for arid zone scorpion *Urodacus yashenkoi* (Birula). This scorpion is entirely nocturnal and digs deep burrows which resulted in the amelioration of daytime temperatures; its behaviour was consequently the antithesis of that found for *G. godeffroyi*. Shorthouse did not compare his estimates of RMR with those expected from the mean ambient air temperature but it is possible to compute the expected values from the data he presented. The calculation is made for a fifth instar male scorpion and compared with the detailed estimates Shorthouse made using a simulation model which related the position of the scorpion in the burrow to the soil temperature profile. Over the 340 days compared (Table 2) the scorpion had a respiratory cost 120% of that expected from the ambient ground level screen temperatures.

Many ectothermic animals especially leaf dwelling insects, may be expected to depart widely from the ambient air temperature (Wellington, 1950). When exposed to radiant heat, equivalent to that obtained from the sun on a clear summer day, leaf surface temperatures may exceed the ambient air temperature by 8°C and if the plant is under water stress by as much as 13°C (Burrage, 1971). Some orthoptera are known to thermoregulate and may even require high temperatures to produce fertile eggs (Papillon *et al.*, 1972). Some cicadas (Homoptera) exhibit both endothermic and heliothermic temperature regulation and maintain their body temperature close to 40°C (Heath *et al.*, 1972). In addition many sessile intertidal invertebrates may obtain high temperature during emersion (Davies, 1970).

While the effect of maintaining other than ambient temperatures was marked in the scorpion and the spider, there are a number of cases where the use of mean air temperatures has been fully justified. These cases apply to aquatic (Hughes, 1970; Lawton, 1971) or litter inhabiting species (Phillipson, 1967) where thermal gradients within the range of the species were small and the influence of direct solar radiation absent. Clearly each species must be assessed according to its habitat and the extent of the animals

Table 2. Oxygen consumption by a fifth instar male scorpion, *Urodacus yashenkoi*, calculated using detailed positional and temperature records and using the mean ambient air temperature on each field trip

Field trip* Number	Interval (days)	Mean ambient air temperature* (°C)	Oxygen consumption (ml day ⁻¹) calculated using:	
			Detailed records*	Mean air temperature†
4		25.75	4.421	3.030
5	43	19.25	2.079	1.575
6	48	9.85	0.833	0.611
7	45	8.30	0.657	0.523
8	44	12.25	0.835	0.778
9	44	26.00	1.954	3.107
10	39	17.95	1.797	1.382
11	55	26.35	4.582	3.218
13	22	—	—	—
Sum			17.158	14.224
Σ consumption × interval			668.87	558.61

* From Shorthouse (1971).

† Calculated from data in Shorthouse (1971).

excursions through thermal gradients. Even in apparently simple cases, such as the nocturnal scorpion, the effective temperature may depart widely from the mean ambient temperature.

The effect of reproduction on the resting metabolic rate

Egg sac production in *G. godeffroyi* and egg sac weight reached a peak in January and February (Humphreys, 1976). The oocytes matured rapidly in the spring and most mature females had some mature oocytes throughout the breeding season except while carrying egg sacs (Fig. 3).

The number of mature females used in the experiments to determine RMR was sufficient to examine for the effect of gonad condition in July, September and December. The variance in the data increased with the onset of the breeding season (July/September, $F = 16.26$, $P < 0.002$; September/December, $F = 3.98$, $0.05 > P > 0.02$) as would be expected from the data in Fig. 3 if gonad condition had an effect on respiration. There was, however, no significant change in respiration level.

Gonad condition has been shown to have marked effects on the respiration rate in Phalangids (Phillipson, 1963) terrestrial isopods (Phillipson & Watson, 1965) and ticks (Aboul-Nasr & Bassal, 1972). The variation found in *G. godeffroyi* was similar to that for the isopod cited above. However, data from *Lycosa T-insignita* indicate that any observed increase in respiration was associated with increased feeding rather than gonad condition *per se* (Miyashita, 1969). As Phillipson (1963) and Phillipson & Watson (1965) used animals straight from the field the changes in respiration which they attributed to gonad condition may have resulted from the increased respiration associated with food assimilation.

The effect of activity and feeding on the resting metabolic rate

Respiration rates increased two to five times in *G. godeffroyi* during carbon dioxide respirometry when

the spiders were made to run (Humphreys, 1973). Despite detailed field activity records (Humphreys, unpublished) it was impossible to determine the respiratory cost of locomotion in the field.

The respiration rate in *L. T-insignita* increased by from 3 to 6 times in active rather than stationary spiders (Miyashita, 1969). In the theraphosid *Aphonopelma sp.* the increase was about 4-fold but the scope for activity was temperature dependent and decreased as the upper thermal limit was approached (Seymour & Vinegar, 1973).

The regressions relating the respiration of recently fed spiders to the spider weight are presented in Table 3 and compared with the regressions derived from unfed spiders at the same or similar temperatures. The regressions for fed spiders have the same slope as those from the unfed spiders at 20 and 30°C but there is a significant upward displacement of the intercept (Table 3). The regression for fed spiders at 35°C has a similar slope to the regression for unfed spiders at 40°C and again there is an upward displacement of the intercept. The Q_{10} relationships for these post feeding regressions are Q_{10} (20–30°C) = 1.72 and Q_{10} (30–35°C) = 2.63. The former index is similar to that obtained from the RMR regressions but the latter is nearly twice as great; the temperature of this experiment was close to the temperature at which spiders thermoregulated in the field (Humphreys, 1974).

The post-fasting respiration in *Lycosa pseudoannulata* fell below the pre-fasting level by 16.3%. In *L. T-insignita* the level similarly fell to 41 and 46.7% in males and females respectively but only increased after feeding to 81 and 70% respectively, of the pre-fasting level (Miyashita, 1969). The latter condition corresponds to the feeding conditions used for *G. godeffroyi*. The respiration could therefore be expected to increase further after prolonged feeding. The increase observed in *G. godeffroyi* varied from 159 to 219% depending on the temperature and the increase was greater than those reported by the

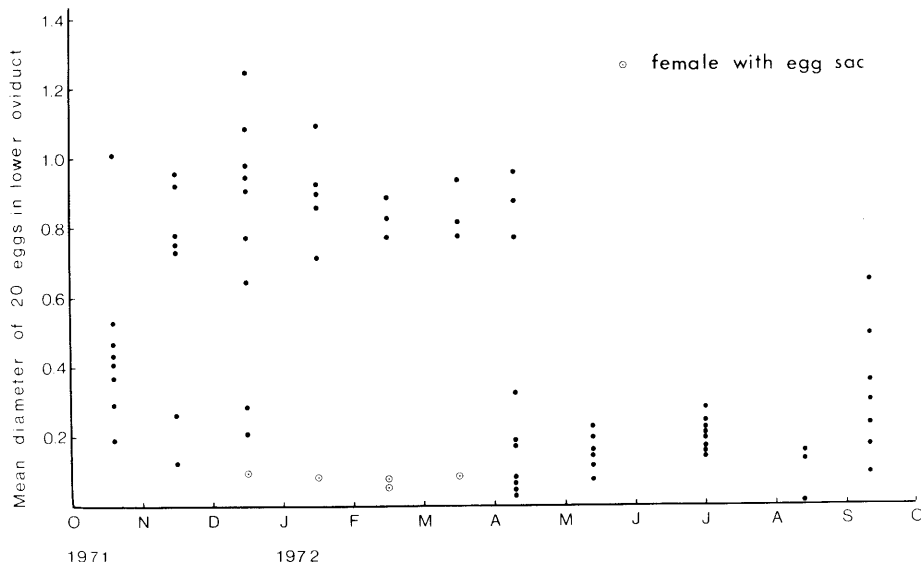


Fig. 3. The breeding condition of female *Geolycosa godeffroyi* as indicated by the diameter of the oocytes (mm). Each point represents the mean diameter of 20 oocytes from the lower oviduct of an individual spider.

Table 3. Regressions relating the oxygen consumption ($\log_{10} Y \mu\text{l hr}^{-1}$) to the live weight ($\log_{10} X \text{ mg}$) of recently fed *G. godeffroyi*

Temperature (°C)	N	Regression equation	Standard error		Correlation coefficient	t_c	P
			Intercept	Slope			
20	28	$Y = 0.868 X - 0.296$	0.173	0.068	0.929	12.76	<0.001
30	13	$Y = 0.934 X - 0.349$	0.536	0.193	0.824	4.83	<0.001
35	14	$Y = 0.781 X + 0.320$	0.259	0.109	0.900	7.16	<0.001

Comparison of the regression lines from recently fed spiders with RMR data for the same temperatures

Data compared	Bartlett's χ^2 test for residual variance			Test of parallelism			Test of identity		
	D.F.	χ^2	P	D.F.	F	P	D.F.	F	P
20°C RMR with 20°C fed	1	3.10	0.1-0.05	1, 51	0.32	0.75-0.5	2, 51	19.06	<0.001
30°C RMR with 30°C fed	1	0.36	0.9-0.5	1, 70	0.24	0.75-0.5	2, 70	4.17	0.025-0.01
40°C RMR with 35°C fed	1	1.75	0.5-0.1	1, 35	0.11	0.75-0.5	2, 35	11.91	<0.001

authors cited above. Respiration in *Tarentula kochi* increased over the pre-feeding rate by 360% during ingestion, and was still elevated by 167 and 133% after 1 and 4 days respectively (Hagstrum, 1970).

The respiration rate of *Pardosa laura* Karsch fell by nearly 45% during the first four days of starvation but then stayed roughly constant until 10 days. In *Trochosa ruricola* (Degeer), *Lycosa pullata* (Clerc.) and *Pirata latitans* (Blackw.) respiration dropped for the first 1-4 weeks of starvation but then began to rise (Nakamura, 1972).

Itô (1964) examined the effect of feeding on the house fly *Musca d. domestica* but could detect no difference in the respiration rate before and after feeding. Oxygen consumption in *Daphnia pulex var. pulicaria* Forbes did not alter with starvation over 6 days but the respiratory quotient dropped from 1.13 to 0.71 (Richman, 1958). This 31% drop in R.Q. could account for the effects observed by both Itô (1964) and Miyashita (1969), particularly as they measured carbon dioxide production which is a more variable index of metabolic heat loss than the uptake of oxygen. Such a large change in R.Q. could not account for the magnitude of the effect observed in *Pardosa laura*, *T. kochi* or *G. godeffroyi*. Furthermore the R.Q. in *Tarentula kochi* did not vary over the period of the experiments (Hagstrum, 1970) but neither the experimental conditions nor the error were specified. Nevertheless there can be little doubt that spiders exhibit a period of markedly increased respiration following feeding; this would be at least partly due to specific dynamic action (Brody, 1964; McGilvery, 1970).

Closing remarks

It has been shown that cycling temperatures over a range of about 17°C (11.7-29.3°C) on a sine wave with 24 hr period increases respiration to 135% of that expected from the RMR respiration measurements presented here (Humphreys, 1975b). In addition *G. godeffroyi* (Humphreys, 1975b) as well as other lycosids (Anderson, 1970) undergo metabolic rate compensation or acclimation and this provides an explanation for the season variation in respiration rates described by the multiple regression equation presented above.

The respiratory relations of *G. godeffroyi* have, in this paper, been compared with others for lycosids

and shown to be generally consistent with them where the conditions used by the various investigators overlap. Despite respiration measurements being conducted over the complete temperature and weight range found in the field there is still considerable variation about the RMR (in parenthesis following) introduced by other factors. Activity (2.0-4.9), feeding (1.59-2.19), cycling temperatures (1.35) and seasonal variation (1.2) occur together introducing a potential error factor of at least 5.15 (i.e. $2.0 \times 1.59 \times 1.35 \times 1.20$). As the Q_{10} varies with temperature and with the weight of the spider, field estimates cannot be made from mean temperatures either of the environment (even if appropriate) or the spider, but must be calculated from a knowledge of actual temperatures throughout the day and at representative intervals through the year.

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