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The Food Consumption of a Wolf Spider, *Geolycosa godeffroyi* (Araneae: Lycosidae), in the Australian Capital Territory

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Summary. A method is described to measure the food consumption of a wolf spider, *Geolycosa godeffroyi*, in the field. The method is based on a calibration curve relating the food consumed in 14 days to the production of components of the excreta, mainly guanine, in the subsequent 7 days. The method was used to measure the food consumption of the spiders in the field over one year. Compared with many arthropods, *G. godeffroyi* feeds at a high rate but this is probably a reflection of its habit of behavioural thermoregulation.

Introduction

Wide differences can be obtained in the respiration rates of animals in the laboratory according to the experimental method used and the prior history of the individual (Phillipson, 1962, 1963; Itô, 1964; Phillipson and Watson, 1965; Miyashita, 1969; Anderson, 1970; Moeur and Eriksen, 1972; Weatherley, 1972). Estimates of the energy flux through populations in the field should therefore not rely on the extrapolation of laboratory derived respiration rates but should incorporate some major parameter measured in the field along with production. It is to this end that field estimates of consumption are required.

The development of a method to measure food consumption is outlined in this paper and it is used to estimate the annual consumption of the wolf spider *Geolycosa godeffroyi* (L. Koch, 1865) in the Australian Capital Territory. This species is burrow dwelling and undergoes behavioural thermoregulation on sunny days throughout the year (Humphreys, 1974). The temperature differential is such that the estimated annual metabolic heat loss approximates that expected from the mean monthly maximum ambient temperatures rather than the mean monthly temperatures (Humphreys, 1973).

A number of techniques have been used to investigate the feeding of spiders in the field. Turnbull (1966) counted all the insects present in the spiders' habitat and determined which were potential prey. A number of authors have observed spiders feeding in the field to qualify the food type (Kuenzler, 1958; Turnbull, 1960; Edgar, 1969, 1970) and Kajak (1967) counted the number of prey trapped in webs to estimate food consumption. Edgar (1969) attempted to quantify the feeding of *Pardosa lugubris* (Walckenaer) by determining the proportion of spiders with prey in their chelicerae and the time required for food handling. He assumed

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that spiders were equally likely to feed during any part of their active period but later found that this was not true (Edgar, 1970). A number of workers have confined spiders to field cages and counted the number of prey at the start and end of the experiment (Dabrowsha-Prot, 1966; Dabrowsha-Prot *et al.*, 1966; Luczak and Dabrowsha-Prot, 1966; Breymeyer, 1967; Hagstrum, 1970b).

Biological turnover rates of radionuclides were measured by Van Hook (1971) and used to determine the partitioning of several elements through a grassland ecosystem. The food consumption of forest floor spiders in general was estimated using radionuclide techniques in a forest system totally labelled with ^{137}Cs (Moulder and Reichle, 1972). The method relies on a direct relationship between the radionuclide elimination rate and the temperature. In both Van Hook (1971) and Moulder and Reichle (1972) this was true within the temperature range 15–25° C but Moulder (1969) showed that the elimination rate at 30° C was lower than at 15° C in *Lycosa* sp. The elimination models used were consequently only applicable within a temperature range considerably narrower than that found in the field.

With *G. godeffroyi* the monitoring of faeces and food remains in the burrows was prevented by the accumulation of debris in the burrows, the spiders' ability to almost totally ingest soft bodied insects and the low pH of the soil. At low pH the guanine component of the faeces was soluble. The approach adopted was stimulated by Avery's (1971) work on the lizard *Lacerta vivipara* Jacquin, in which he collected animals in the field and measured the production of faeces in the laboratory, under near natural conditions. This led to the derivation of a calibration curve relating the amount of food consumed by *G. godeffroyi* in 14 days to the production of components of the excreta, mainly guanine, in the subsequent 7 days. This calibration curve permitted an estimate of the amount of food consumed by a spider in the 14 days prior capture in the field (see "Discussion").

Guanine

Guanine has long been considered as the main nitrogenous excretory product of spiders but it was first specifically identified by Vajropala (1935). It was the only purine present in the excreta of those mites and spiders that have been examined (McEnroe, 1961; Anderson, 1966), although scorpions may have several (Kanungo *et al.*, 1962). Examination of the literature showed that while there may be wide interspecific variation in the proportion of guanine in the excreta, intraspecific variation was low (Vajropala, 1935; Schmidt *et al.*, 1955; Atkinson and Chorlton, 1956; Rao and Gopalakrishnareddy, 1962; Anderson, 1966; Horne, 1969) and it could possibly be used as the basis for field determinations of the total excreta. Guanine accounted for 94% of the nitrogen in the excreta of *Lycosa urbana* (Haggag and Fouad, 1965) and between 79% and 87% in the excreta of *L. lenta* Hentz (Anderson, 1966).

Methods

The method routinely used for the determination of guanine in the excreta of *G. godeffroyi* was that of Vischer and Chargaff (1948) and partly as modified for use on crude arachnid excreta by Anderson (1966). Spider excreta were dissolved in 1N KOH and aliquots diluted with the same solution until the final concentration was in the required range. The sample

was scanned between 250 and 300 nm in a spectrophotometer (Shimadzu, model MPS-50) and the optical density read at 273.5 nm. The scanning allowed the location of major interference peaks which occasionally caused departure from the normal form of the guanine curve. Such samples were checked for contamination and rejected if none was shown. Twelve samples were rejected in this way and it is thought that the interference peak was caused by uric acid. The concentration of guanine in the sample was determined against a standard curve run against pure guanine (Sigma) and read at 273.5 nm.

Excreta were collected by maintaining the spiders with water but no food in plastic drinking cups for the required length of time. The spiders were removed from the cups and the latter stored at −15° C until analysis. Nitrogen determinations were made by a micro-kjeldahl method on some of the excreta samples. Enzymatic determination of guanine followed the method of Kalchar (1947).

All drying was conducted at 35° C to constant weight in a vacuum oven with dry air flowing through it. The caloric content of samples was determined in either a Phillipson (1964) type micro-bomb calorimeter or a Gallenkamp Ballistic Bomb Calorimeter according to the sample size. All weighings were performed on either a Mettler analytical balance to 0.1 mg or a Cahn Electro-Balance to 0.001 mg as appropriate to the sample size.

Feeding and Delayed Excreta in the Laboratory

Spiders were collected from the field, weighed and placed in incubators under the appropriate temperature regime in individual containers. Water was provided and every second day the spiders were fed with weighed prey, comprising from one to four animals, to produce a graded feeding regime for spiders of similar size. The spiders were transferred to clean containers the next day and the food remains collected, dried and the dry weight equivalent of the food eaten was determined. The spiders were fed for 2 weeks (7 feeds) and then transferred to clean containers and taken on a car journey of a length equivalent to the distance from the field site to the laboratory (*cf.* Avery, 1971). On return to the laboratory the spiders were maintained under constant illumination at 20° C and 70% to 80% relative humidity for seven days with water but no food. They were provided with clean containers on the second and the fourth days. The spiders were removed from the cups which were stored at −15° C until the excreta were analysed.

Experiments were conducted using mealworms (*Tenebrio molitor* L.) as the food source at 10, 20 and 30° C and with the temperature cycling from 8–34° C on a sine wave with a 24 hr period. Experiments using bushflies (*Musca vetustissima* Walker) and lycosids (*Alopecosa* sp.) as the food source were conducted at 20° C. Relative humidity under the cycling temperature regime varied from 60–92% and the lighting in all the experiments was on a 12 hr light, 12 hr dark schedule.

Excreta from Spiders Collected in the Field

Spiders were collected in the field at about monthly intervals from October 1971 to September 1972 and maintained for 7 days at 20° C in the laboratory with water but no food. The excreta produced from the time of collection to the end of the 7 day period were collected and stored at −15° C until analysed by the methods outlined above.

Field Trial on the Calibration Curve

In April 1972 a field experiment was conducted to determine the validity of the laboratory derived calibration curve. Spiders were established in plaster replicas of the burrows in an area adjacent to the field site (Humphreys, 1973). The burrows were covered with a cone, half of which consisted of gauze and half of a clear plastic. The cone excluded prey organisms and permitted free air circulation and access by the spiders to direct sunlight and allowed them to maintain their normal thermoregulatory behaviour. The spiders were removed from their burrows, placed in containers and fed on mealworms and the amount of food eaten determined. They were returned to their burrows and the cones replaced. They were fed in a similar manner a week later and returned to the laboratory after the end of the second week. They were

Table 1. Determination of the relationship between "guanine" estimated spectrophotometrically (A mg ml^{-1}) and guanine determined enzymatically (B mg ml^{-1})

Sample	A	B	B/A
1	0.237	0.122	0.513
10	0.147	0.093	0.631
53	0.495	0.299	0.652
52	0.320	0.207	0.647
11	0.155	0.116	0.745
40	0.552	0.402	0.728
32	0.263	0.144	0.549
44	0.154	0.097	0.627
41	0.360	0.254	0.706
3	0.224	0.140	0.627
5	0.176	0.101	0.572
			$\bar{x} = 0.636$
			S.E. $= 0.021$
			$n = 11$

maintained at 20° C and the excreta produced during the subsequent 7 days collected and analysed. Seventeen spiders were originally established but as many of the cones had been displaced, only seven were recovered for the collection of excreta.

Results and Discussion

Initial testing for possible interference in the spectrophotometric determination of guanine from the crude excreta was conducted by the repeated addition of a known amount of guanine to the excreta. The relationship differed from that obtained by the addition of guanine to a solution of guanine indicating that interference was occurring from some fraction of the crude excreta samples. Determinations made by the spectrophotometric method are henceforth referred to as "guanine".

The enzymatic determinations were undertaken to determine the constancy of this interference. The results in Table 1 show that the interference was fairly consistent and that guanine accounted for an average of 0.636 (S.E. = 0.021) of "guanine" estimated by the spectrophotometric method. This finding was supported by the analysis of the total nitrogen present in samples of the excreta collected throughout the year and covering the complete size range of *G. godeffroyi*. In Fig. 1 the concentration of "guanine" in each sample is plotted against the total nitrogen and line "B" represents the expected relationship between nitrogen and guanine if the guanine alone accounted for all the nitrogen in the excreta (guanine contains 46.6% nitrogen). The data fall well above the expected line and are divergent from it. This relationship was unexpected and indicated that guanine accounted for a much lower proportion of the nitrogen than published figures. Furthermore the divergence of the data from the expected line would be difficult to explain, for it implies that whatever the size of the spider a large defaecation would have a greater proportion of nitrogen than a small one. By applying the correction factor determined in the enzymatic analysis relating "guanine" to guanine a new expected line ("A") was calculated. This line does not diverge

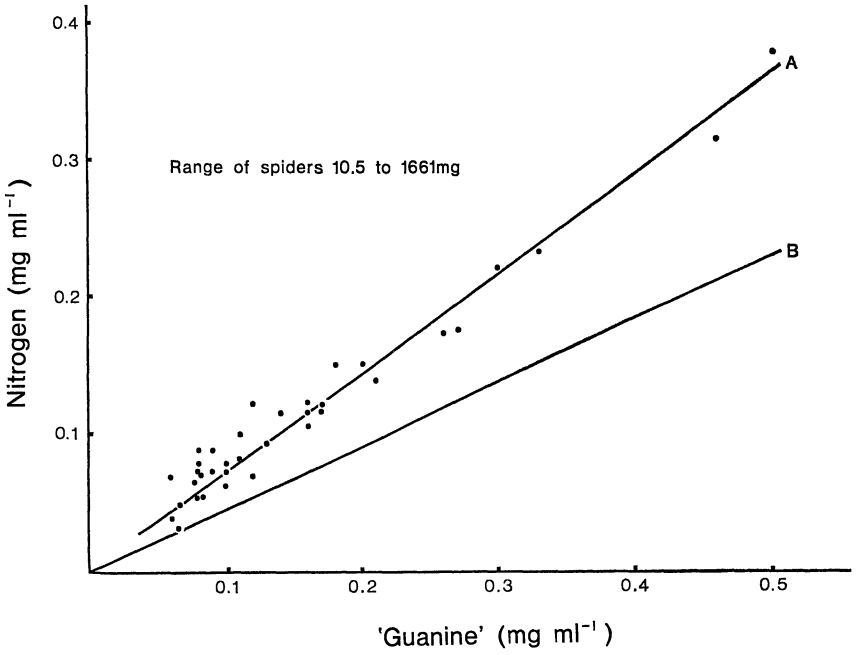

Fig. 1. The relationship between "guanine" estimated spectrophotometrically and the total nitrogen contained in the excreta. Line *B* represents the expected relationship if "guanine" accounted for all nitrogen in the excreta. Line *A* was derived from line *B* by correcting it according to the enzymatically determined relationship between guanine and "guanine"

from the data and indicated that guanine contained most of the nitrogen in the excreta. The variability of the data around this expected value results from sample variation and experimental error but a large proportion of it can probably be attributed to the presence of silk in the excreta increasing the amount of nitrogen in the sample. Samples of excreta collected by hand without appreciable quantities of silk indicated that guanine contained an average of 87.8% (S.E. = 3.99) of the total nitrogen in the excreta (Table 2).

In the experiments using mealworms as the food source the period of 14 days feeding followed by 7 days of excreta collection was chosen after a preliminary trial. The results were analysed by taking progressively longer feeding periods until the best relationship was found. Similarly the collection of the excreta was added into the analysis for longer periods of collection, either 2, 4 or 7 days. The best relationship was found using the entire 7 feeds (14 days) and the full 7 days of excreta collection. It is possible that a better relationship could be established using longer periods for both feeding and excreta collection.

The details of the experiments relating mealworm consumption in 14 days to the production of "guanine" in the subsequent 7 days are presented for each experimental condition in Fig. 2. The individual regression lines are significant ($P<0.001$) and analysis of variance shows that the lines are parallel ($0.75>P>0.5$) and an not significantly displaced ($0.5>P>0.25$) (Table 3). A new

Table 2. The proportion of nitrogen and guanine in the excreta of *G. godeffroyi*

Sample	A	B	C	D	E	D/E × 100
1	1.287	0.560	0.356	0.165	0.21	78.6
2	0.806	0.663	0.422	0.196	0.20	97.8
3	0.682	0.471	0.300	0.139	0.21	66.1
4	3.023	2.044	1.300	0.603	0.73	82.6
5	2.380	2.432	1.547	0.717	0.76	94.4
6	0.754	0.422	0.268	0.124	0.15	82.9
7	1.303	1.060	0.674	0.313	0.34	91.9
8	0.315	0.291	0.185	0.086	0.08	107.2
9	1.394	1.054	0.671	0.311	0.35	88.8
						$\bar{x}$ = 87.88
						S.E. = 3.99
						n = 9
Guanine controls						
10				0.649	0.64	98.6
11				0.674	0.67	99.4

A = weight of excreta (mg). B = spectrophotometric determination of "guanine" (mg). C = B adjusted by correction factor (0.636) to estimate guanine. D = guanine nitrogen calculated from C. E = determination of the total nitrogen. D/E = estimated guanine nitrogen as a percentage of total nitrogen determination.

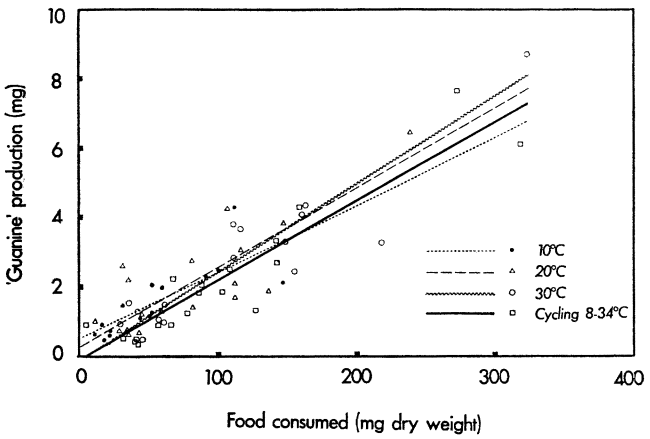

Fig. 2. The relationship between the food consumed by *G. godeffroyi* in 14 days under four different temperature conditions and the production of "guanine" in the following 7 days during which the spiders were maintained at 20° C and not fed

regression line was therefore calculated for the pooled data and it accounted for 83.5% of the variance in the data. Adding the weight of the spiders to the regression (Table 4) shows that weight had a significant effect on the relationship ($t = 2.822$, $0.01 > P > 0.001$) but accounted for only another 1.84% of the variance. The latter equation was used as the calibration curve in further calculations taking $b_0 = 0$.

Table 3. Regressions relating the food consumed by *G. godeffroyi* in 14 days (X mg) to the "guanine" produced in the following 7 days (Y mg) during which the spiders were maintained at 20° C and not fed

Treatment	N	Regression equation	Standard error		Correlation coefficient	t_s	P
			Intercept	Slope			
10° C	19	$Y=0.0192\ X+0.534$	0.2112	0.0037	0.787	5.27	<0.001
20° C	20	$Y=0.0229\ X+0.277$	0.3131	0.0027	0.894	8.16	<0.001
30° C	18	$Y=0.0159\ X+0.759$	0.6609	0.0040	0.691	10.50	<0.001
Cycling temperature	19	$Y=0.0227\ X-0.124$	0.2689	0.0021	0.934	10.78	<0.001
Pooled	76	$Y=0.0227\ X+0.187$	0.1364	0.0012	0.914	19.39	<0.001

Analysis of variance on the data before pooling

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
3	3.33	0.5–0.1	3, 68	0.54	0.75–0.5	6, 68	1.11	0.5—0.25

Table 4. Multiple regression equation relating "guanine" production (Y mg) in 7 days without food at 20° C to the dry weight of food consumed (X_1 mg) in the previous 14 days and the final live weight of the spider (X_2 mg)

Form of the equation:

$$Y=b_0+X_1b_1+X_2b_2$$

where;

	Standard error	t	
$b_0=-0.0641$			
$b_1=0.0222$	0.00114	19.552	$P<0.001$
$b_2=0.000392$	0.000139	2.822	$0.01>P>0.001$
$n=76,\ r^2=0.853$			

Analysis of variance:

	D.F.	M.S.	F	
Regression	2	110.922	212.63	$P<0.001$
Residual	73	0.522		

Spiders and bushflies were used as food sources to test for the effect of prey type on the calibration curve derived above. Both items of prey were utilised by *G. godeffroyi* in the field and they were chosen for their large difference in nitrogen content. As the calibration curve relied on the determination of a component of the excreta which is largely nitrogen, variation in the nitrogen content of the prey could be expected to influence the calibration curve. Bushflies have a low and

Table 5. The nitrogen content of various food species and their remains after the spider had finished feeding

Food source	Total nitrogen content (% dry weight) Entire			Remains			NU/MR[a]	Nitrogen in food consumed (%)
	Mean	S.D.	*N*	Mean	S.D.	*N*		
Bushfly	7.51	0.33	6	10.06	1.32	2	0.233	6.71
Mealworm	8.71	0.11	4	10.32	0.27	4	0.270	8.33
Lycosa sp.	12.21	0.56	4	12.92	0.51	4	0.249	12.08

[a] Proportion of food killed but not eaten.

Table 6. Statistics relating the food consumed by *G. godeffroyi* from three different prey types in 14 days (*X* J) to the production of guanine in the following 7 days (*Y* mg)

Food source	*N*	Regression equation	Standard error of slope	*R*	*P*	t_s against a slope of 0.0	*P*	t_s against mealworm slope	*P*
Mealworms	76	$Y=0.000837\,X+0.187$	0.000044	0.914	<0.01	19.39	<0.001	—	—
Lycosids	9	$Y=0.000677\,X+0.252$	0.000200	0.788	0.05–0.01	3.39	0.01–0.001	0.801	0.5–0.4
Bushflies	10	$Y=0.000849\,X+0.053$	0.000132	0.915	<0.01	6.44	<0.001	0.087	>0.9

spiders a very high nitrogen contentb ut the food remains left after the spider had fed on them were of similar nitrogen content (Table 5). Furthermore qualitative differences in the form of the nitrogenous excretion exist between the spiders and insects. The latter excrete uric acid whilst the former excrete guanine, both of which may interfere with the calibration curve if they were ingested by *G. godeffroyi*.

The results of the two additional feeding experiments were expressed on an energy basis and the slopes compared with the slope of the calibration curve derived from feeding mealworms to the spiders expressed on the same basis. Neither slope is significantly different from the original calibration (Table 6 and Fig. 3).

The laboratory experiments indicate that the derived calibration curve is applicable under a wide range of conditions of temperature, humidity, spider weight and prey type. The calibration curve was based entirely on "guanine" and the difference between "guanine" and guanine would have no effect on the calibration. The relationship is empirical and an understanding of the reasons underlying it would require an examination of the dynamics of food movement through the spiders. Of particular relevance to the delayed release of excreta in spiders are the intestinal caecae and the stercoral pocket as they may buffer the movement of food and excreta respectively through the spider. The production of excreta during the feeding period was highly temperature dependent.

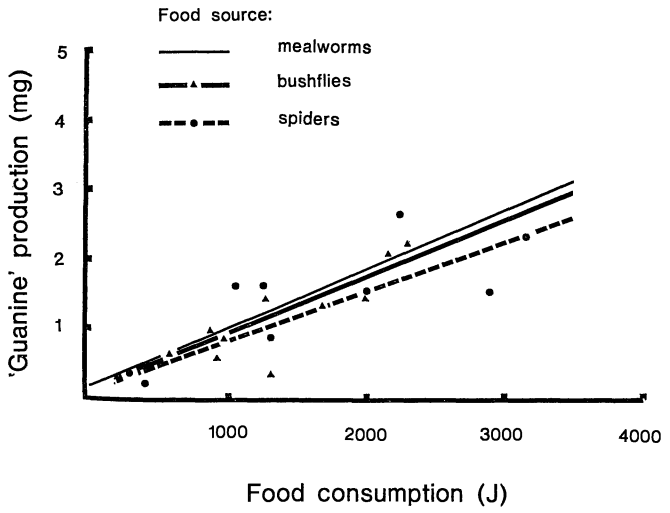

Fig. 3. The relationship between the food consumed by *G. godeffroyi* in 14 days from three different prey types to the production of "guanine" in the following 7 days

Table 7. Results of the experiment to test the applicability of the laboratory derived feeding calibration curve to the field

Spider reference	Spider live weight (mg)	Food consumed (mg dry weight)	"Guanine" produced in 7 days (mg)	Expected "guanine" (mg)	Produced / Expected (%)
1005	974.0	31.4	1.742	1.079	161.4
1007	871.7	27.0	0.796	0.941	84.6
1009	101.2	9.32	0.279	0.247	113.0
1010	74.3	7.32	0.147	0.192	76.6
1013	485.9	15.5	0.351	0.535	65.6
1015	1017.0	19.7	1.297	0.836	155.1
1016	281.1	12.2	0.218	0.381	57.2

Mean = 101.9
$n = 7$

The field experiment confirmed the validity of the laboratory derived model when applied to the field in April 1972 (Table 7) and the model is assumed to be applicable to the field under all conditions at which it was tested in the laboratory.

Determination of Food Consumption in the Field

Between October 1971 and September 1972, 333 spiders were collected in the field and the production of "guanine" over the subsequent 7 days determined in 324 cases. Plotting the "guanine" production against the spider weight showed a curvilinear relationship. The variability in the data was consistent up to a spider weight of about 800 mg. Above this weight the data became very variable due to the inclusion of breeding females. The data were accordingly analysed separately

Table 8. Regressions relating the weight of spiders weighing less than 800 mg ($\log_{10} X$ mg) to the production of "guanine" ($\log_{10} Y$ mg) in the 7 days following collection from the field

Month of collection		N	Regression equation	Standard error		Correlation coefficient	P	F	D.F.	P
				Intercept	Slope					
1971	Oct.	37	$Y=0.6693\,X-1.7197$	0.211	0.102	0.743	<0.01	43.22	1, 35	<0.001
	Nov.	24	$Y=0.6574\,X-1.5670$	0.303	0.135	0.721	<0.01	23.82	1, 22	<0.001
	Dec.	30	$Y=0.8286\,X-1.9149$	0.211	0.091	0.865	<0.01	83.00	1, 28	<0.001
1972	Febr.	23	$Y=0.6173\,X-1.5600$	0.252	0.120	0.747	<0.01	26.59	1, 21	<0.001
	March	19	$Y=0.8957\,X-2.0107$	0.255	0.115	0.883	<0.01	60.47	1, 17	<0.001
	April	23	$Y=0.8211\,X-2.3789$	0.568	0.274	0.548	<0.01	9.01	1, 21	0.01–0.005
	May	12	$Y=0.7740\,X-1.7244$	0.297	0.137	0.873	<0.01	31.98	1, 10	<0.001
	June	17	$Y=0.8619\,X-1.8379$	0.052	0.096	0.973	<0.01	269.90	1, 15	<0.001
	July	28	$Y=0.7052\,X-1.6246$	0.108	0.203	0.789	<0.01	42.98	1, 26	<0.001
	August	14	$Y=0.6514\,X-1.7753$	0.337	0.160	0.761	<0.01	16.47	1, 12	<0.001
	Sept.	16	$Y=0.7937\,X-1.9100$	0.280	0.133	0.848	<0.01	35.79	1, 14	<0.001

Bartlett's χ^2 test for residual variance; $\chi^2=136.16$ with 10 D.F., $P<0.001$.

Table 9. "Guanine" production by *G. godeffroyi* greater than 800 mg in weight during the 7 days following collection from the field

Collection date		N	Spider weight (mg)		"Guanine" (mg)	
			Mean	S.D.	Mean	S.D.
1971	Oct.	9	1322.64	319.22	3.718	2.280
	Nov.	6	1364.07	171.56	4.311	2.730
	Dec.	7	1530.24	384.53	6.732	6.435
1972	Febr.	11	1469.99	427.39	5.452	4.131
	March	8	1429.44	369.09	8.546	8.068
	April	12	1591.23	413.43	3.240	3.507
	May	9	1255.83	289.54	6.594	3.374
	June	5	1127.00	180.79	4.462	4.413
	July	3	1326.70	291.05	3.857	0.745
	August	6	1240.20	334.77	5.576	4.282
	Sept.	4	1440.28	499.05	2.146	1.858

for those spiders greater and those less than 800 mg which was about the division between the juveniles and the mature females.

The results for 244 spiders <800 mg were available for analysis and the regressions of spider weight against "guanine" production for each collection period are presented in Table 8. In all months save April ($0.01>P>0.001$) the regressions were highly significant ($P<0.001$) but the data cannot be pooled due to their heterogeneity ($P<0.001$). The regression for each month was therefore used to estimate the food consumption at the mean annual weight of each size class of spider. The food was assumed to have an energy content of 21.52 J mg dry

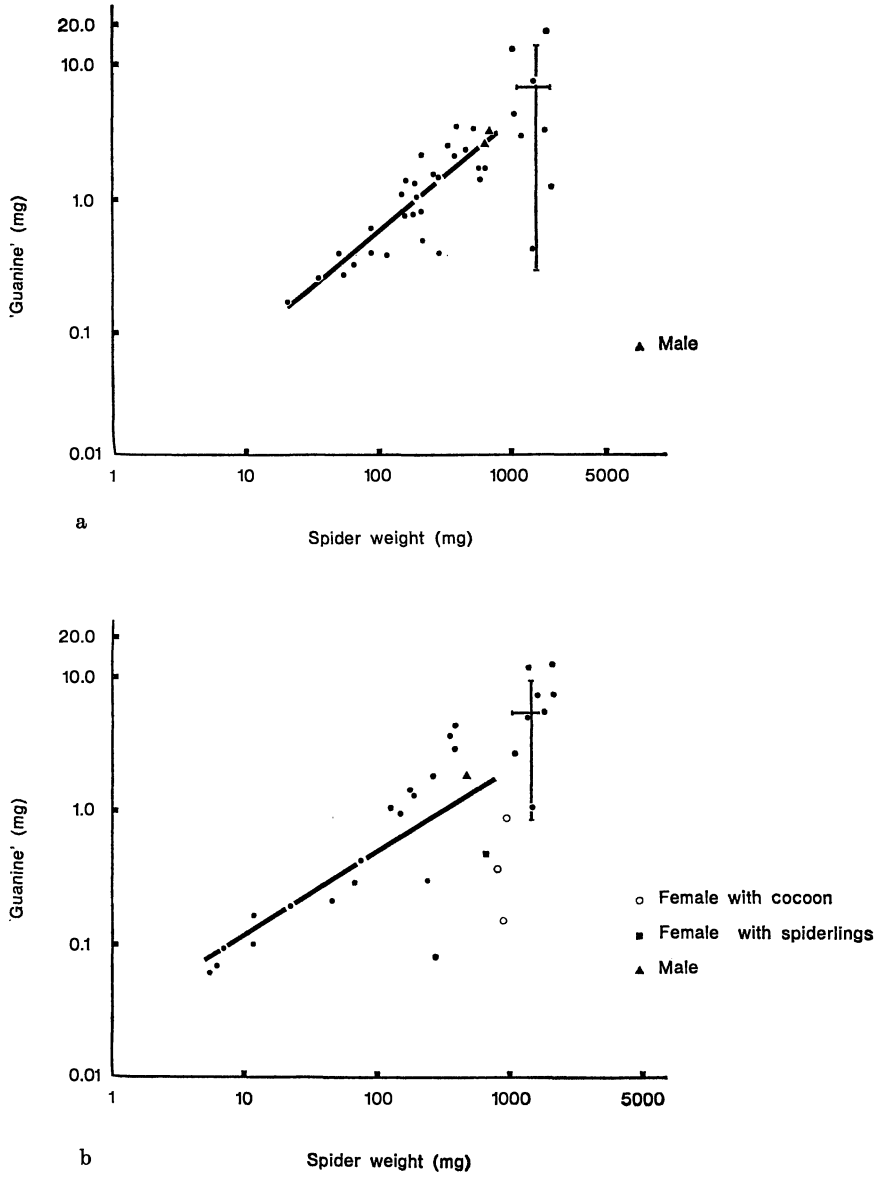

Fig. 4a and b. The relationship between the weight of *G. godeffroyi* collected in the field and the production of "guanine" in the following 7 days when maintained at 20° C in the laboratory. (a) represents the data from spiders collected in December 1971 and (b) those from spiders collected in February 1972. The regression lines from spiders less than 800 mg (Table 8) are drawn through the data and the standard deviations of the data are shown for spiders greater than 800 mg (Table 9)

Table 10. Estimated average daily food consumption from October 1971 through September 1972. Size classes 7–15 occur in the population throughout the year but the smaller size classes are present in the population for only part of the year

Size[a] class	Food consumption		Feeding interval days
	J day^{-1}	mg day^{-1}	
1	2.232	0.103	1.50
2	2.666	0.123	1.79
3	4.157	0.193	2.08
4	5.735	0.266	2.28
5	9.559	0.444	2.32
6	13.42	0.623	2.74
7	16.62	0.772	3.23
8	21.62	1.01	3.54
9	31.19	1.45	4.03
10	42.20	1.96	4.48
11	62.60	2.91	5.14
12	84.12	3.91	5.69
13	113.6	5.28	6.30
14	149.9	6.97	6.48
15	306.2	14.23	6.78

[a] The size classes are based on the mean growth increment in the field and are thus similar to instars (Humphreys, 1973).

weight $^{-1}$ which is the mean energy content of arachnids and insects cited in Cummins and Wuycheck (1971, p. 33).

80 spiders were available for the greater than 800 mg size group and consumption was estimated from the mean weight of each monthly collection of spiders and the mean "guanine" production. The means were applied to the multiple regression model to estimate food consumption (Table 9).

The data from two months only are presented in Fig. 4 together with the regression lines for the data from spiders less than 800 mg and the standard deviation of the data for those spiders greater than 800 mg. Fig. 4b shows the influence of cocoon carrying on the production of excreta. Spiders carrying cocoons or spiderlings produced little excreta indicating that they ate little. This is supported by other work which has shown that lycosids rarely eat while carrying cocoons (Miyashita, 1968).

In Table 10 the estimated food consumption of an individual of each size class throughout the period covered by the field collection is presented. In the right hand columns the mean dry weight equivalent of the food eaten over the year is presented together with the feeding interval. The latter is based on a mean prey size of 0.25 the spider weight, a prey water content of 75% and 100% ingestion.

The original calibration curve was derived under a wide range of conditions in the laboratory, in particular under realistic conditions of cyclic temperature which may affect various rate functions in the laboratory (Humphreys, 1973). The laboratory testing together with the agreement found in the field experiments allow the extrapolation to the field with confidence under the conditions tested.

In the field, however, *G. godeffroyi* was subjected to temperatures in excess of 34° C on clear days throughout the year due to its habit of thermoregulating. The mean daily spider temperature never exceeded 23° C and in winter (June – August 1972) was between 8.0 and 8.4° C but exceeded 12.5° C in all other months. The effect of the mean temperature falling below 10° C was not determined as the spiders would not feed at these low temperatures. The other main factor not examined in the laboratory was the effect of activity on the relationship. Although *G. godeffroyi* is a fairly sedentary animal in the field it has been shown that subtle change in activity may have marked effects on respiration (Humphreys, 1973). Despite the potential shortcomings of the calibration curve it has finer confidence limits, was more rigorously tested and tested over a far wider range of conditions than similar calibration curves used to estimate field rate processes in poikilotherms (Van Hook, 1971; Moulder and Reichle, 1972).

In *G. godeffroyi* the relationship between the dry weight of food consumed per day (Y mg) to the dry weight of the spider (X mg) is described by the equation:

$$Y = 0.1327\, X^{0.761\ (\text{S. E.} = 0.0085)},\ n = 15,\ r = 0.999.$$

The power function in this equation would be expected to follow one of the proposed models relating physiological processes to the animal's weight. The slope of the equation is different from 1.0 ($t = 27.63$, $P<0.001$) and from that describing a surface area relationship where $b = 0.67$ ($t = 11.067$, $P<0.001$). It is not different from the power function derived by Hemmingsen (1960) relating the standard metabolic rate of numerous organisms to their body weight where $b = 0.756$ ($t = 0.550$, $0.9>P>0.5$). Humphreys (1973) showed that the slope describing the respiration to weight relationship for *G. godeffroyi* did not differ from the upper confidence limit of the general slope derived by Hemmingsen. The relationship between the mean daily food consumption and the weight of the spider is realistic.

Reichle (1968) measured the food consumption of eleven species of arthropod detritivores inhabiting a forest floor and found that the relationship between food consumption and the animal's weight was close to the "Van der Drift constant". This relates food consumption to the 0.67 power of the dry body weight and indicates a surface area relationship. This "constant" may, however, vary with the physiological state of the species (Phillipson, 1960) and cannot be considered as a real constant.

In Fig. 5 the estimated daily food consumption by *G. godeffroyi* is compared with estimates reported in the literature for other species. The power functions calculated from the data vary between 0.58 and 0.76 and there is considerable vertical displacement between the various estimates. The data for the dipteran, *Hedriodiscus truquii* (Bellardi) were based on wet weight estimates (Stockner, 1971) and conversion to dry weight would bring the line closer to the data for *G. godeffroyi* but the intercept of the regression would still be displaced upwards. These data were obtained for two hot spring populations, one of which had a mean temperature (35° C) close to that at which *G. godeffroyi* thermoregulated.

The comparisons are only partially realistic as the assimilation efficiency of the species varied considerably and was greatest in *G. godeffroyi*. The vertical displacement of the data for *G. godeffroyi* above the data for most other species

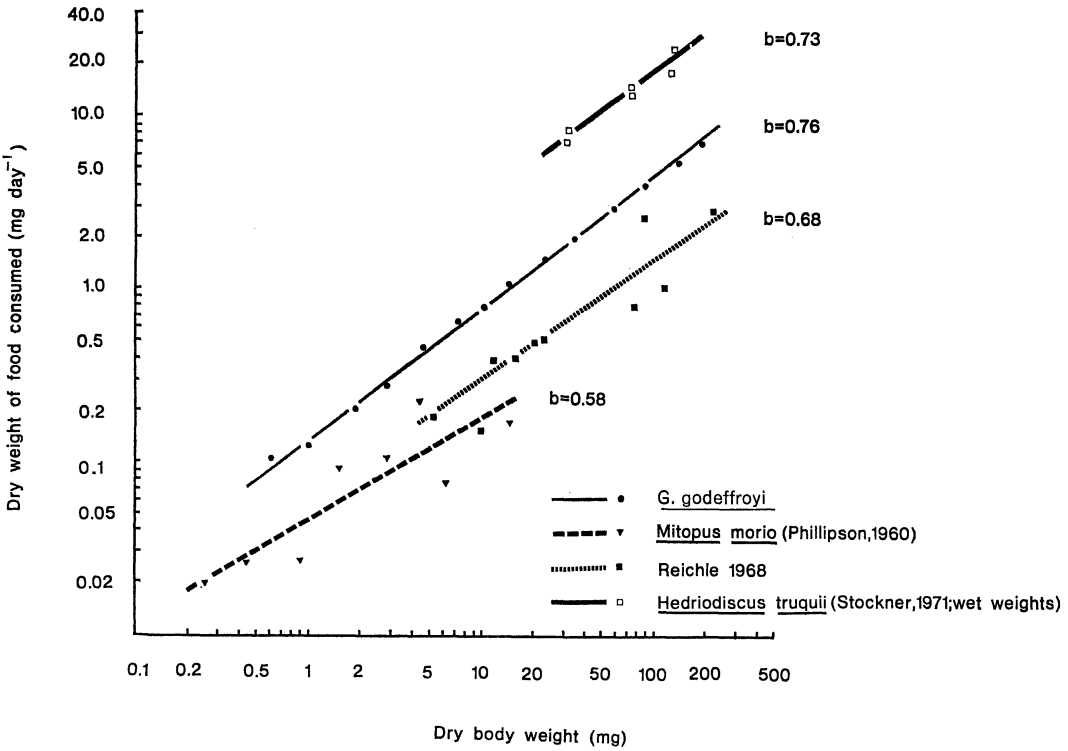

Fig. 5. The estimated relationship between the body weight and food consumption in *G. godeffroyi* compared with the same relationship calculated for other species from data available in the literature. Th edata for *Mitopus morio* have been recalculated assuming 75% water in predator and prey

was probably related to the high growth rate in the former. *G. godeffroyi* increased in weight up to 3000 times over two years compared with an increase of from 300 to 400 times in *Pyrrhosoma nymphula* (Sulz.) (Odonata) over a similar period (Lawton, 1971) and an increase of 70 times in the phalangid, *Mitopus morio* (F.) over one year (Phillipson, 1960). In addition *G. godeffroyi* probably had high winter maintenance requirements associated with thermoregulation.

A particularly interesting comparison can be made with the lizard *Lacerta vivipara* studied by Avery (1971). This species is heliothermic and thermoregulates in a similar manner to *G. godeffroyi* but at a lower temperature (30.2° C). The species is also carnivorous and with a high assimilation efficiency. Avery determined the relationship between food consumption (F mg dry weight day $^{-1}$) and the weight of the lizards (W g) in the field. He obtained the relationships for sunny days; $F = 21.8\ W^{0.74}$, and on days of changeable weather; $F = 12.4\ W^{0.70}$ (Avery defined the units incorrectly in his summary). The power functions of these relationships are close to that derived for *G. godeffroyi* of 0.76. Avery could separate the data from sunny and changeable days and the data for the latter,

after conversion to dry weights, lies about one line-width above the data for *G. godeffroyi* at 500 mg dry weight in Fig. 5. The values for *G. godeffroyi* are the mean annual estimates and include all types of wheather and as the mean annual cloud cover in Canberra is 4/8 the data are most comparable to Avery's changeable-weather relationship.

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