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(Araneae: Lycosidae)

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THE POPULATION DYNAMICS OF AN AUSTRALIAN
WOLF SPIDER, *GEOLYCOSA GODEFFROYI*
(L. KOCH 1865) (ARANEAE:LYCOSIDAE)

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INTRODUCTION

Most of the work conducted on the biology of spiders has been descriptive and population dynamics have seldom been mentioned. The only serious attempts to examine the dynamics of lycosid populations are Edgar's (1971a, b) study of *Lycosa (Pardosa) lugubris* Walck. in Scotland and the briefly reported study of *Tarentula kochi* Keyserling in California (Hagstrum 1970, 1971).

This general lack of work on a conspicuous and important component of terrestrial communities (Van Hook 1971; Moulder & Reichle 1972) may seem a strange omission from field studies. A brief examination of some of the characteristics of spiders may help to explain it. Spiders are not commonly harmful to or overtly beneficial to man. They have poorly marked life stages, are difficult to age, and sex determination in the immature stages is not possible. The life history is commonly long and normally covers a wide range of size; *Geolycosa godeffroyi* (L. Koch) hatches at 1 mg but may reach 3000 mg as a mature female. Their predatory habits result in generally low population densities; mature female lycosids have been found at densities of 1.3–5.8 m⁻² (Edgar 1971a), 3.5 m⁻² (Brey Meyer 1967) and 0.33 m⁻² (Hagstrum 1970) and at 10 m⁻¹ of shore line (Hackman 1957). This problem was exacerbated with *G. godeffroyi* as adult females occurred in favourable areas at a density of about 0.01 m⁻².

Preliminary study

G. godeffroyi construct burrows without a trap-door and the depth varies from about 4 to 18 cm dependent on the size of the occupant and the season. The spiders can maintain their body temperatures above that of the ambient air temperature throughout the 24 h by basking in the sun during the day and withdrawing down the burrows at night (Humphreys 1974).

The larger species of lycosids inhabiting the northern hemisphere have about a two-year life cycle and pass through from 7 to 10 instars. Due to the large size of *G. godeffroyi*, I expected it to have about a three year life cycle. Observation indicated that the population density was low compared with European populations. The accumulation of discarded egg sacs in adult burrows indicated that burrows were inhabited for more than one year by the females or were reused by different individuals in successive years, implying a certain permanency in the population.

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DISTRIBUTION AND HABITAT

Geolycosa godeffroyi occurs in about a 200-km wide coastal strip from Bundaberg in Queensland to Port Lincoln in South Australia. It follows a similar zone from Esperance to Northampton in Western Australia (Hogg 1900; Musgrave 1931; Butler 1933; Hall 1968; R. J. McKay, personal communication).

Observations in the east of New South Wales and the Australian Capital Territory indicate that *G. godeffroyi* inhabits the margins of, and the clearings in, sclerophyll forest. It was found at high density only in small patches but more extensively in rough pasture that was reverting to bush. The only extensive dense populations were in artificially maintained clearings such as those beneath high-tension transmission lines. In these areas the woody perennials were periodically removed by hand or herbicide treatment. The resulting vegetation was generally a rough grassland, with a varying cover of shrubs, dependent on the interval since the last clearing. The natural habitat is probably similar to these conditions but ephemeral due to the succession of vegetation types.

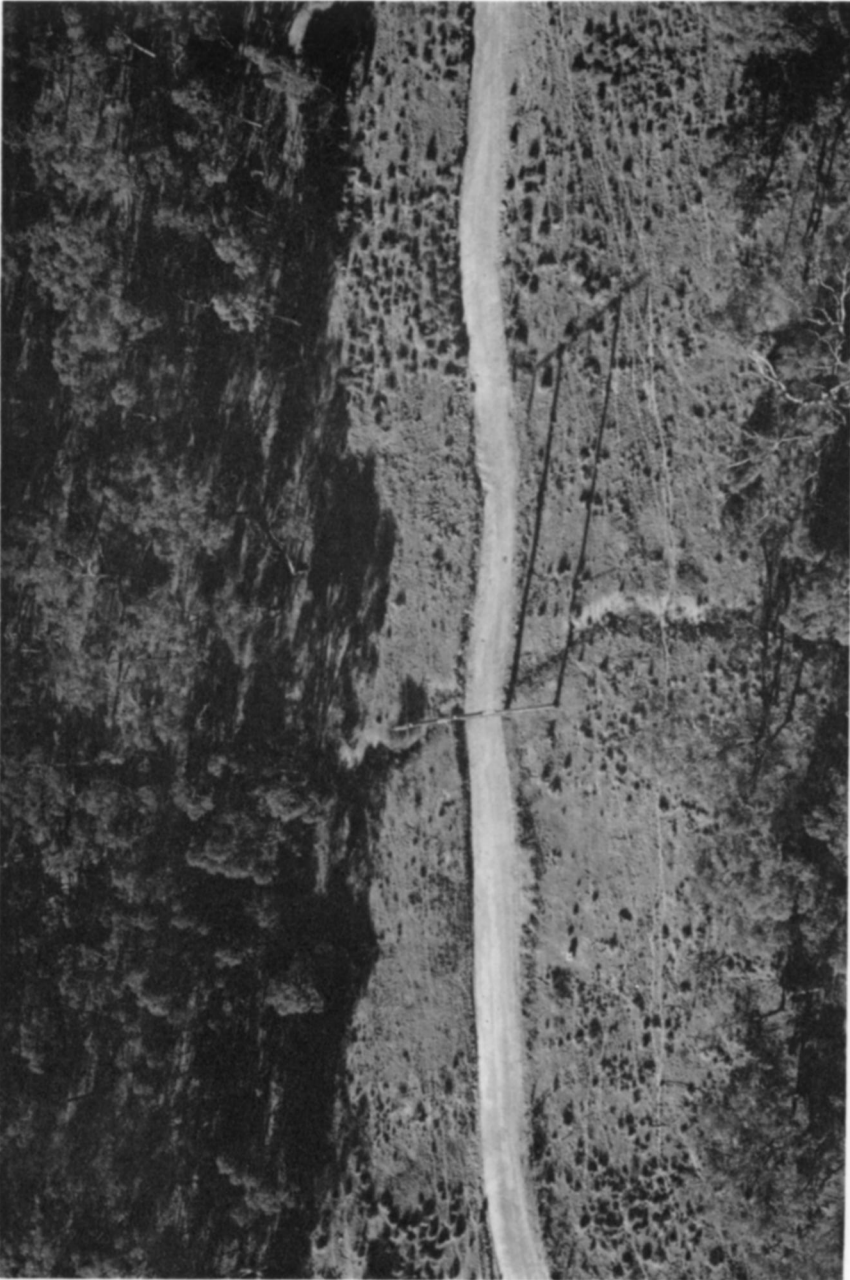
The Kowan field site

All field work was conducted in a clearing maintained beneath a high-tension transmission line (line no. 977, Canberra–Queanbeyan, operated by the Electricity Commission of N.S.W.) through natural forest in the Kowan Forest Reserve, Australian Capital Territory (Plate 1). The strip was cleared and the timber stacked and burnt in 1954. The clearing was treated with 2.4.5T herbicide every two years. After two or three treatments effective control was obtained and the interval between treatments extended to four or five years. The last treatment was applied selectively in March 1971 (R. J. Whitehurst, personal communication). In the region of the field site, two small clumps of shrubs had been treated. The field site comprised a roughly rectangular 1330 m² area to the western side of the transmission line clearing (Plate 1).

The area is situated on the edge of the deeply dissected Cullarin Horst and has a skeletal red-yellow podzolic soil overlying decomposing shale (Pryor & Brewer 1954). The shale intermingled with the thin soil on the site, except on the lower western fringe. The clearing passed along an abrupt transition between dry sclerophyll woodland on the upper side (*Eucalyptus rossii* R. T. Bak et H. G. Sm.—*E. mannifera* Mudie community) and savannah woodland (*E. melliodora* A. Cunn.—*E. bridgesiana* R. T. Bak community) on the lower side. This transition reflected the change in relief as the steep hillside levelled into the valley floor. Within the clearing the vegetation was dominated by the grasses *Themeda australis* (R. Br.) and *Poa trivialis* L. which were kept short by the grazing of sheep and wallabies. The tussock grass *Danthonia pallida* R. Br. occurred in patches. Occasional woody perennials formed a sparse shrub layer (*Hibbertia obtusifolia* D.C. (Dilleniaceae), *Cassinia aculeata* R. Br. (Compositae) and *Eucalyptus polyanthemus* Schau. (Myrtaceae). The ground layer contained a scattering of *Marrumbium vulgare* L. (Campanulaceae), *Rumex acetosella* complex (Polygonaceae) and *Onopordum acanthium* L. There was sparse summer growth of *Wahlenbergia stricta* Sweet (Campanulaceae) and *Hypochoeris glabra* L. (Compositae), forming a very low herb layer.

METHODS

Routine sampling commenced in May 1971 and continued at about monthly intervals until November 1972, except during the winter of 1972 when the interval was increased



Aerial view of the field site at Kowan. The site occupied the area on either side of the gully to the lower (western) side of the track.
Photograph by Royal Australian Air Force.



View of the field site to show the sparse vegetation cover. The white cups were located above occupied spider burrows.
Photograph by W. F. Humphreys.

to about six weeks. At each sampling, from five to seven days of trapping were conducted depending on the weather and a total of 112 trapping days were spaced over a period of 599 days. A further sample was taken in September 1974 in the same general area by digging and hand collection.

Trapping

Preliminary trials indicated that the burrowing section of the population could be adequately trapped. Several methods were evaluated to sample the non-burrowing juveniles and a quadrat method finally adopted. As Edgar (1971a) found, the problem of sampling the juvenile section of the population was never satisfactorily overcome.

The burrowing habit offered a number of advantages as well as disadvantages. It excluded the use of capture and recapture methods due to non-random dispersal through the population. At the same time it would permit the accurate determination of environmental parameters (Humphreys 1974), the relocation of individuals to determine growth, and an accurate record of fecundity. As the instars were expected to last from six to eight weeks (Edgar 1971b; Hagstrum 1970, 1971), individual marking was used to measure the growth rate instead of relying on cohort analysis (Miyashita 1969; Edgar 1971b). This was especially important due to the low population density and patchy distribution of *Geolycosa godeffroyi*, as spiders from adjacent areas may be in markedly different stages of development at a given time of the year (Vlijm, Kessler & Richter 1963).

A plastic tube of appropriate size and length was inserted into the top of the burrow and a glass jar or vial inverted over the top (T. J. Done, unpublished). The spider could climb up the inner surface of the tube, which was covered with matt black paint but not up the outside, which was not painted. Spiders leaving the burrow were unable to return and were prevented from escaping by the glass jar. Many of the spiders not caught in the trap were caught by rapid removal of the tube before the spider retreated down the burrow, and others by the use of forceps. A proportion of the spiders could not be trapped or induced to leave their burrows, but could be seen at the burrow entrance and their size estimated. Details of this are presented later.

The time of clearing traps depended on the season so as to prevent heat stress in the summer and frost induced mortality in the winter. After collection, spiders were maintained in an insulated box to protect them from temperature extremes, processed at night, on site, and returned to the burrows the next morning.

No spiders above size class 8 were found during the day out of association with a burrow. The smaller size classes of *G. godeffroyi* were commonly active during the day or were found sheltering in the vegetation.

An indication of the efficiency of finding burrows can be gained from the number of burrows found at different times during a field trip. On any field trip the first two days were devoted both to searching the site and placing the traps. The site was searched twice on each subsequent day of the trapping period save the last, when no search was made.

The field trips from August 1971 to November 1972 covered a period of 457 days during which 388 new burrows were found on the field site (Table 1). Burrows were found at an average rate of 0.85 burrows per day. During the first two days of the field trips 336 burrows were found and during the other forty days of searching a total of only fifty-two new burrows were located. During these 'second search days' one might expect $40 \times 0.85 = 34$ new burrows to have been established by the spiders whereas fifty-two burrows were found, leaving a discrepancy of $52 - 34 = 18$ burrows unaccounted for during the entire period.

The efficiency of the trapping procedure in recording the presence of an occupant in the burrow was determined by excavations of burrows following trapping in another area. Trapping recorded an average of 93·8% of the spiders present (Table 2). No adjustment was made to the population data to account for this inefficiency but all the unrecorded spiders were of the smaller burrowing size classes.

Table 1. *The number of new burrows found on the Kowan field site*

	Month of field trip	Number of new burrows found on the first two days	Number of new burrows found on subsequent days
1971	Aug.	28	5
	Sept.	15	4
	Oct.	37	6
	Nov.	28	7
	Dec.	30	3
1972	Jan.	17	0
	Feb.	30	3
	Mar.	3	2
	Apr.	11	2
	May	29	4
	June	17	3
	July/Aug.	30	6
	Sept.	23	3
	Oct.	20	1
	Nov.	18	3
	Sum	336	52
	No. of days	30	40

Table 2. *Test of the efficiency of the trapping method used for Geolycosa godeffroyi*

	Month of test		
	November 1971	January 1972	May 1972
Total no. of traps set	74	61	28
No. of spiders trapped	11	3	6
No. caught by hand	14	4	3
No. seen and not caught	7	13	8
No. of burrows remaining	42	41	11
No. of burrows excavated*	39	32	11
No. of <i>G. godeffroyi</i> found during excavation	2	1	1
Percentage not recorded in census	6·25	5·0	5·88

Mean percentage recorded in census = 94·5.

* The discrepancy here is caused by some burrows being impossible to excavate due to their association with rocks, trees or root systems.

Quadrat methods

The population of the smaller size classes was vacuum sampled monthly in 48 to 80, 0·25 m² pseudorandomly located box quadrats taken at peak activity periods (Edgar 1971a), morning or evening in summer and in sunshine in winter; results were pooled monthly for analysis. The spiders were weighed and measured and returned to the area from which they were collected.

This technique was tested for efficiency by adding marked individuals to the quadrats 1 h before sampling and recording the number recovered. The spiders were marked ventrally to avoid biased sorting.

In the first series of tests five individuals were added to each of twelve 1-m² quadrats. In six quadrats all were recovered; in four one was lost, and in the remaining two two were lost, giving a recovery of 86.7% of the marked spiders. In the second series in which marked spiders were added to a random selection of routine quadrat samples, 78.3% of the spiders were recovered (Table 3). The test quadrats were located by the same pseudo-random methods used for the routine quadrats and their association with tussocks of the grass *Danthonia pallida* had a similar probability. In practice few of the routine quadrats and none of the test quadrats were located on these tussocks. I would expect to recover no small spiders from quadrats located on tussocks.

Handling procedure

In a study involving repeated handling it is undesirable to use a narcotic. Accordingly, a restraining apparatus, which allowed the measurement of, and the application of marks to spiders, was used. Marks were applied with enamel paint (Humbrol, cf. Edgar 1971a) to the sternum and the ventral surface of the coxae and spiders larger than size class 4 could be individually coded by this method. The marks applied were not visible from the

Table 3. *The recovery of marked spiders added to routine quadrats*

Date	No. added	No. recovered
1972 Jan.	2	2
Feb.	8	7
Mar.	4	4
Apr.	4	3
May	5	2
Total	23	18

Percentage recovered = 78.3.

side or above so that differential capture or predation would not be expected. Marked spiders moulted without difficulty but the frequency of moulting in *Geolycosa godeffroyi* resulted in the loss of marks from a high proportion of the population between field trips.

RESULTS AND DISCUSSION

The data from each burrow were compiled into a calendar of catches (Petruszewicz & Andrzejewski 1962) for that burrow. In the few cases when a marked individual was known to have moved to another burrow a calendar was compiled for the individual.

Estimation of the size class of spiders seen but not trapped

Many of the spiders on the field site were seen but not captured and their size was estimated by eye. Some spiders that had been allotted a size class were later caught in the same field trip without the traps having been removed in the intervening period. These data were analysed to check the accuracy of the estimated size class and they yielded the relationship,

$$y = 2.49 + 0.76x; \text{S.E.}b = 0.046, r = 0.86, n = 124,$$

where y is the actual size class and x is the estimated size class (Fig. 1). The slope of this regression is different from 1.0 ($t = 5.27$, $P < 0.001$) and all estimates of size class in the field were adjusted to the nearest size class indicated by the regression.

Growth increment of spiders in the field

During the field programme a number of spiders that had previously been measured, ecdysed during the handling procedure. These spiders were kept for 24 h to allow the cuticle to harden, after which there was little variation in the carapace width during the instar (cf. Miyashita 1968). The spiders were then remeasured and the growth increment calculated for the sixty-seven spiders involved, which covered a range of carapace widths from 1.65 to 8.5 mm. The mean growth increment of 1.162 (S.E. = 0.0035) was in close

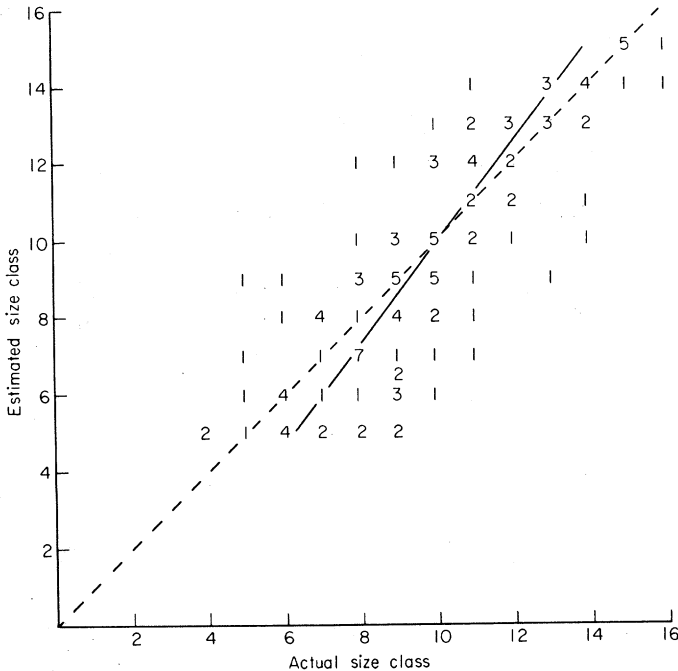


FIG. 1. The relationship between the estimated size class of spiders seen in their burrows and the actual size class determined after subsequent capture. The numbers on the figure represent the number of data points in each position. The fine broken line represents the null line if the actual and estimated size classes were equal and the bold line the regression through the data.

agreement with the mean growth increment of 1.160 determined for the first seven instars of spiders fed every two days in the laboratory at 25° C. The spiders' size and the time of year had no effect on the growth increment. This field-derived growth increment was used to establish artificial size classes for *Geolycosa godeffroyi* which are used throughout this work (Table 4).

Using this classification on spiders handled during the field programme in which the sex could be determined (sub-adults and adults), the males had a mean size class about one less than the females (Table 5) and this agrees with laboratory work which has shown that male lycosids mature at an earlier instar than the females (Bonnet 1930; Miyashita

1968; Edgar 1971a). Females recorded in size class 16 were all in the extreme lower range of that size class and were considered to be large size class 15 rather than small size class 16 spiders.

Growth rate

Weighings were obtained from 1157 spiders taken in traps, quadrats or by hand on and around the field site throughout the year. The seasonal weight changes in any class were

Table 4. *The mean width and range of the size classes of Geolycosa godeffroyi based on the mean field growth increment*

Size class	Mean width (mm)	Limits	
		Lower	Upper
0*	0.905	—	0.97
1	1.038	0.98	1.12
2	1.206	1.13	1.30
3	1.406	1.31	1.51
4	1.630	1.52	1.76
5	1.894	1.77	2.04
6	2.202	2.05	2.37
7	2.559	2.38	2.76
8	2.975	2.77	3.21
9	3.457	3.22	3.7
10	4.018	3.8	4.3
11	4.671	4.4	5.0
12	5.429	5.1	5.8
13	6.300	5.9	6.8
14	7.334	6.9	7.9
15	8.524	8.0	9.2
16	9.908	9.3	

* Size class 0 represents the instar which lycosids pass through while still in the egg sac. The limits for any one size class (N) were taken as the geometric mean between size class N and $N-1$ and between size class N and $N+1$.

Table 5. *The mean size class of those spiders on the Kowan field site in which the sex was determined*

Category	Mean size class	Size class range	N
Sub-females	13.86	13-14	160
Mature females	14.94	14-16	184
Sub-males	13.26	12-14	31
Mature males	13.83	13-14	5

not significant and the mean weight of each size class was determined for all the data (Table 6).

From the calendar of catches for both the individual and the burrow, information was gained on the growth rates of the spiders in two ways. On known individuals the growth rate was calculated directly. Secondly, spiders that were unmarked but of the next higher size class to the individual previously marked in that burrow were assumed to be the same individual, which had moulted in the interval between captures. This assumption was frequently strengthened by the recovery, from the upper region of the burrow, of the

exuvium, which had the mark of the spider previously captured in that burrow. Not all these spiders were caught and weighed, so the rate of change of size class was also calculated for the 517 results available.

For the first method 314 results were available out of the 1121 records of spiders in burrows from October 1971 to October 1972. The data have been divided into summer and winter periods. The winter was from June to September and was the only period in which some of the population showed negative production and the proportion of the population moulting dropped to a minimum (Humphreys 1973). The summer period was taken as the remainder of the year.

The growth rates are presented in Table 7. No growth records were available for the first four size classes and they were estimated by extrapolation as outlined in the footnote to Table 7. The mean winter growth rate was 21.1% of the summer rate and this is used for all size classes in further calculations. Size class 14 has not been divided into winter

Table 6. Mean annual weight data for *Geolycosa godeffroyi* recorded from the Kowan site

Size class	Mean weight (mg)	Standard error	N	95% limits	
				Lower	Upper
1	2.48	0.08	44	2.32	2.64
2	3.52	0.11	42	3.29	3.74
3	6.41	0.21	36	5.98	6.85
4	9.72	0.52	35	8.66	10.79
5	16.50	0.48	68	15.54	17.46
6	27.31	0.84	103	25.65	28.97
7	39.87	0.96	106	37.96	41.78
8	56.95	1.35	132	54.45	59.60
9	93.5	4.8	115	84.1	102.9
10	140.6	4.4	94	131.9	149.2
11	239.1	8.4	73	222.3	255.8
12	355.6	14.2	58	327.0	384.1
13 f	532	29	39	474	590
13 m	671	56	15	559	782
14 f	992	39	63	915	1070
14 m	772	39	18	690	853
15 f	1543	40	111	1464	1622
15 m	1071	52	5	937	1024

f, female; m, male.

and summer rates as the records for this size class are in or close to the winter period. The low values for size class 15 result from considering egg sac production to be negative production and so the rate derived was the net growth rate of the females in both winter and summer.

The data for the summer period and size classes 5-13 have the relationship

$$\log_{10} y = 0.962 \log_{10} x - 1.605, n = 9, r = 0.982,$$

where x = live weight of the spiders (mg) and y = the growth rate (mg live weight day⁻¹). The slope is not different from 1.0 ($t = 0.53, 0.9 > P > 0.5$).

Treatment of the data in this manner may result in an underestimation of the growth rate, for the spiders recaptured with marks may be inherently slower growing. A further estimate of the growth rate was obtained with the addition of those data in which the captured individuals were assumed to be the same individual previously captured but

which had moulted in the interval. Changes from size class 14 to 15 were not included in the analysis. The rate of change of size class was analysed by multiple regression using the size class and weighted seasonal values as predictors. The month of the year was added to multiple regression analyses in a weighted cyclic form. January was set at 6 and the weighting was reduced by 1 each month until June = 1. The weighting was then increased by one each month so that July = 1 and December = 6. This pattern of weighting was found to give the best seasonal weighting to a number of parameters (Humphreys 1973).

Table 7. Mean individual growth rates of *Geolycosa godeffroyi* in the field; (a) 'summer' rates (October–May) and (b) 'winter' rates (June–September)

	Size class	Growth rate (mg day ⁻¹)	Standard error	N	Growth rate from feeding experiment (mg day ⁻¹)	
(a)	1	0.083*			0.071	
	2	0.112*			0.084	
	3	0.180*			0.178	
	4	0.265*			0.236	
	5	0.323	0.125	7		
	6	0.585	0.101	8		
	7	0.783	0.121	15		
	8	1.145	0.161	19		
	9	2.257	0.297	19		
	10	4.303	0.583	22		
	11	5.878	0.748	18		
	12	6.800	0.774	15		
	13	7.108	1.423	20		
	14	2.742	1.640	25		
	15	0.497	1.878	55		
(b)	6	0.155	0.060	10	% Summer rate 25.5	
	7	0.165	0.059	15	21.1	
	8	0.126	0.082	19	11.0	
	9	0.487	0.151	20	21.6	
	10	1.133	0.537	7	26.6	
	11	—				
	12	1.430	0.462	9	21.0	
	13	1.491	0.392	11	21.0	
					Mean	21.1

* These growth rates are calculated from the regression relating the \log_{10} mean growth rate (y) to size classes 5–13 (x) where $y = 0.182x - 1.337$, $r = 0.981$. The column for the feeding experiment denotes the mean growth rate of the instars determined in the laboratory at 25° C on spiders fed every four days.

The resulting model has the form

$$y = 0.0068 + 0.0061 x_1 - 0.513 \times 10^{-6} x_2; n = 517, r = 0.631$$

where y = rate of change in size class day⁻¹, x_1 = season and x_2 = the fourth power of the size class to which the spider moults.

The growth curves for the spiders are plotted in Fig. 2 and are derived directly from the growth rate data assuming a four-month winter period in which the growth rate was 21% of the summer growth rate or from the model which incorporates a correction for the seasonal effects. Model predictions are also plotted assuming the young were released at the earliest and latest part of the breeding season. Considering only the predictions initiated on 16 February the lack of agreement in the lower size classes was expected, as there were

few results for spiders below size class 5. Where the records were sufficient, the agreement between the calculated curves is close. In particular, the agreement between the slopes of the curves is good. Both methods predict that the spiders reach size class 14 in May, which was the period when most of the females reached this stage in the field. The growth of known males cannot be calculated, as few records were available for this sex, they are assumed to have a rate of development similar to the females.

The close agreement between these two methods of calculation is considered to support the general validity of the determination of rate of development and of the artificial division of the data into winter and summer rates.

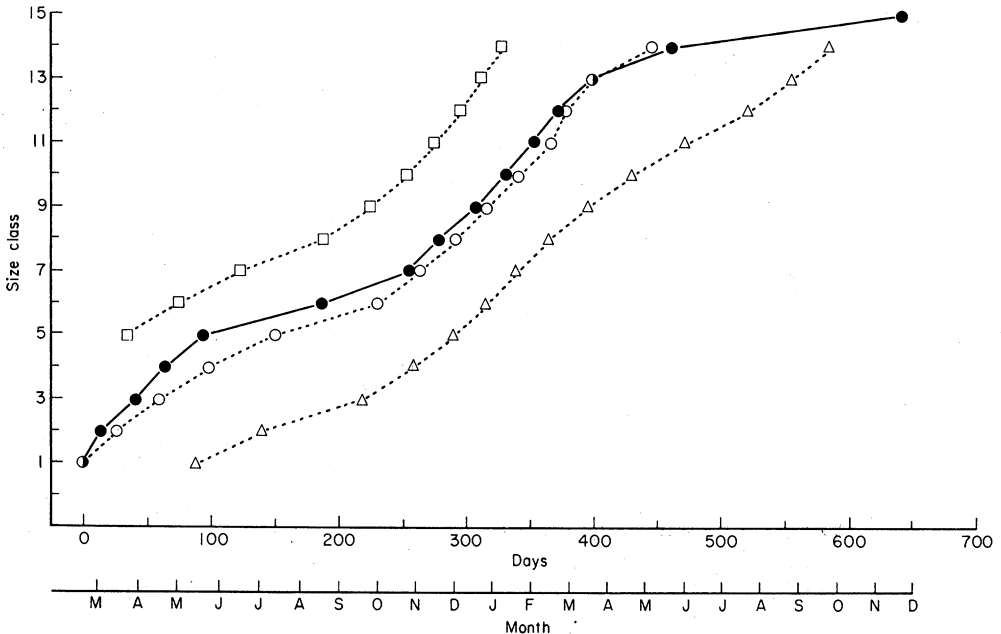


FIG. 2. Growth curve for *Geolycosa godeffroyi* calculated from the actual growth data and from the regression model discussed in the text. —●—, calculated from growth curve assuming the spiders left the mother on February 16, calculated from model; ····○····, released February 16; ····□····, released November 15; ····△····, released May 24. The earlier and late release dates represent the extreme range of the period during which egg sacs were produced.

Duration of the size classes in the field

The actual growth rates were used in conjunction with the mean annual weight data for each size class to estimate its duration in the field (cf. Petruszewicz 1966). Winter growth rates were considered to be 21% of the summer rates for all size classes. The estimates are set out in Table 8 for females only, and were calculated as the mean weight change from the previous size class divided by the growth rate. Mature females were considered to live for 220 days as will be discussed later.

Fecundity

In the field egg sacs are produced from November to April and the young emerge about a month later, having undergone their first moult in the egg sac. The young are carried

on the back of the female for about a week in the laboratory and probably longer in the field. The young resulting from the period of peak production overwinter for the first time at size classes 5–8 and reach the sub-adult stage by the following winter. Females moult to maturity during or after the second winter, produce one or two egg sacs and die. Males moult to maturity at the same time as the females, mate, lose weight and die. Some females produce egg sacs in two successive breeding seasons and provide a gene flow between what would otherwise be two separate populations breeding in alternate years. The females probably all die after the young from their second egg sac have dispersed (Humphreys 1973). Mating takes place in early November after which the males die. The presence of mature males in May indicates that there may be a further period of mating in the autumn as found in *Lycosa carolinensis* Walckenaer (Kaston 1948).

Fecundity was determined by a combination of laboratory and field work. On the field site all egg sacs were weighed and the number recorded. Recently laid eggs weighed 1.81

Table 8. *Duration of the size classes of female Geolycosa godeffroyi in summer*

Size class	Duration of size class (days)
1	12.5
2	25.9
3	18.4
4	25.6
5	33.4
6	21.5
7	23.2
8	32.0
9	20.8
10	22.9
11	19.8
12	26.3
13	64.9
14	200.7

mg (range 1.68–1.97) and there was no consistent trend in the weights of the eggs through the breeding season. Egg sac silk had a mean weight of 22.2 mg (S.E. 3.5, $n = 7$) and these values were used to determine the number of eggs in a weighed egg sac.

The weight of the egg sacs in the field varied with time and reached a peak weight in January and February, the time of peak egg sac production. This relationship is seen in Fig. 3(a) which also shows the estimated number of eggs and of spiderlings reaching the back of the female. This estimate of the production of young provides a firm base from which to estimate mortality.

Under semi-natural conditions the spiderlings were carried by the female for 8.6 days (S.E. 2.3, $n = 11$) and in the field egg sacs were carried for 3.6 weeks (S.E. 1.1 weeks, $n = 14$) as determined by weekly examination of spiders carrying egg sacs. The duration of both egg sac and spiderling stages was about 4.8 weeks. As the maximum interval between field trips in the breeding season was twenty-five days, it is considered that no egg sacs produced in the field went unrecorded. There is a possibility that some spiders may have produced egg sacs and lost them in the interval between field trips. However, in the laboratory spiders deprived of their egg sacs produced another within two weeks

but these egg sacs were markedly smaller than any found in the field and one had only thirteen eggs. As no similar egg sacs were found on the field site it is probable that none of the spiders lost an egg sac.

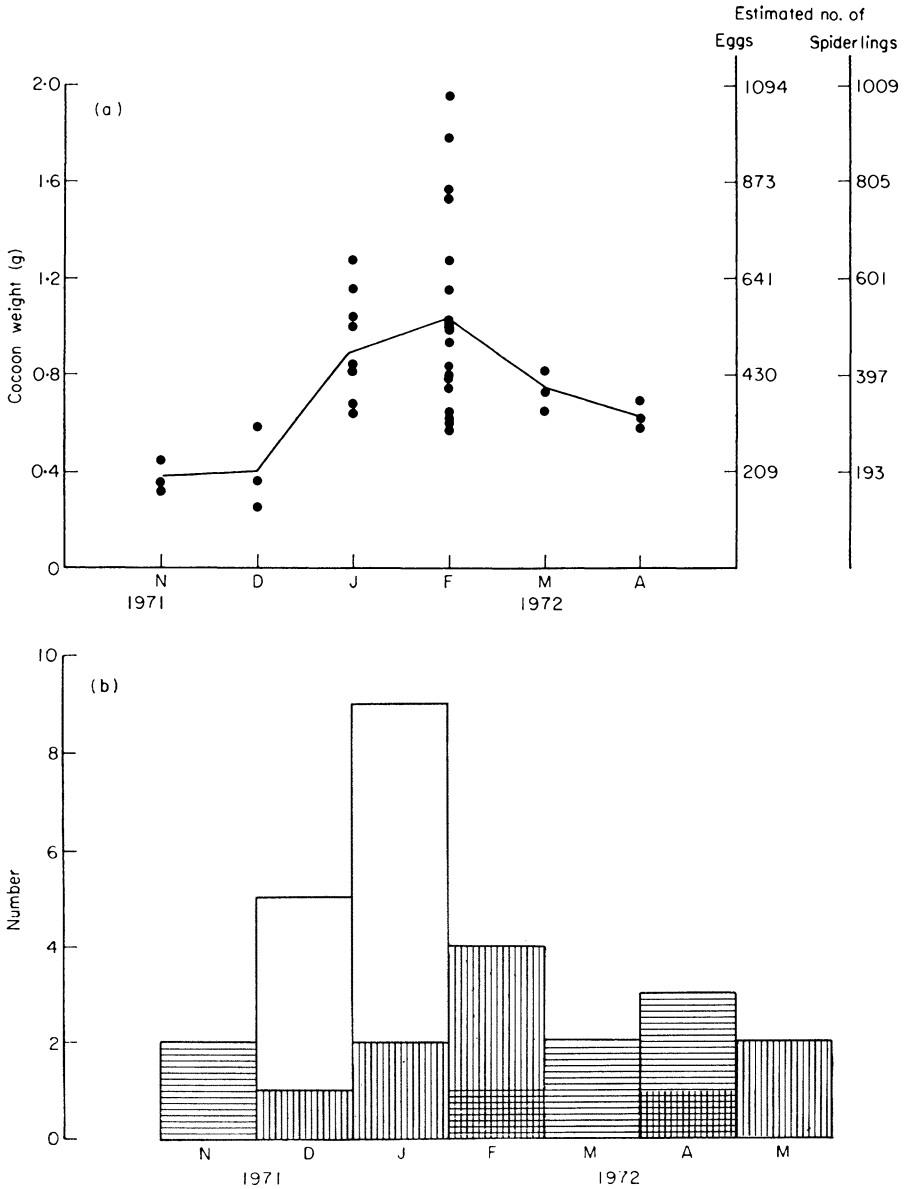


FIG. 3. (a) The weight of all egg sacs from *Geolycosa godeffroyi* during the 1971-2 breeding season. Estimated number of eggs and of spiderlings reaching the back of the female are shown on the right-hand axis. (b) The number of egg sacs recorded on the Kowan field site during the 1971-2 breeding season. Cross hatched areas are known second egg sacs and vertically hatched areas represent records of spiderlings on a female's back.

During the 1971-2 breeding season the production of egg sacs in the field reached a peak in January (Fig. 3(b)). A total of twenty-two egg sacs was produced by an average

of 12.2 females on the field site. The spiderlings were seen on the backs of the females about a month after egg sac production. In Fig. 3(b) the egg sacs indicated as second egg sacs in November were those of females first marked in the previous May and it is possible that they were third egg sacs or more. The second egg sacs recorded in other months were from spiders which were known to have moulted to adults after the winter of 1971 and to have produced their first egg sacs in December or January.

Sex ratio

The method of sampling may have considerable influence on the apparent sex ratio in a number of species of spiders including five species of *Pardosa* (Kessler-Geschiere 1970).

It was not possible to examine the sex ratio in *Geolycosa godeffroyi* on the field site due to the small number of individuals recorded and the possibility of multiple recording of the same individual. As the males died after mating and only the last two instars could be sexed, the sex ratio would be expected to vary seasonally. The sex ratio was therefore examined from spiders collected by digging out the burrows. This should not be biased by the sampling method. An additional sample was taken in the same manner in September 1974.

Table 9. *The numbers of Geolycosa godeffroyi collected for laboratory use in which the sex could be distinguished (χ^2 tests for departure from a 1:1 sex ratio)*

	Month	Females	Males	χ^2	
1971	May	20	5	4.5	0.05 > P > 0.025
	June	1	2	2.91	0.1 > P > 0.05
	July	20	6		
	Aug.	1	0	3.12	0.1 > P > 0.05
	Sept.	10	2		
	Oct.	11	10	0.03	0.9 > P > 0.5
	Nov.	12	10	0.09	0.9 > P > 0.5
	Dec.	23	21	0.18	0.9 > P > 0.5
	Sum	98	56	10.83	0.1 > P > 0.05
1974	Sept.				
	Sub-adults	20	16	0.44	0.9 > P > 0.5
	All	27	17	2.27	0.5 > P > 0.1

Over the entire year there was no significant difference from a 1:1 sex ratio (Table 9) but on a monthly basis the departure was significant in May. Earlier reports of highly biased sex ratios in spiders are yielding to later studies which use appropriate sampling methods at the time of male activity and have shown sex ratios close to parity (Hackman 1957; Vlijm *et al.* 1963).

Population densities

The number of spiders living in burrows on the field site at each field trip is recorded in Fig. 4. The records include the data from 943 spiders that were trapped on the site and 540 spiders that were seen but not trapped and their size class estimated. In addition, 100 spiders which were probably *G. godeffroyi* were known to be present in burrows but no size or species determination was possible (mainly in June of both 1971 and 1972 when the activity of the spiders was reduced by cold weather).

The results of the quadrat sampling are summarized in Fig. 5. The numbers of the small size classes on the field site were estimated by multiplying the mean density by the area of the site.

The combined data from the quadrat and trapping programmes are presented in Table 10 showing the estimated number of spiders on the field site. These estimates are considered to represent the situation on the field site on the first day of any field trip.

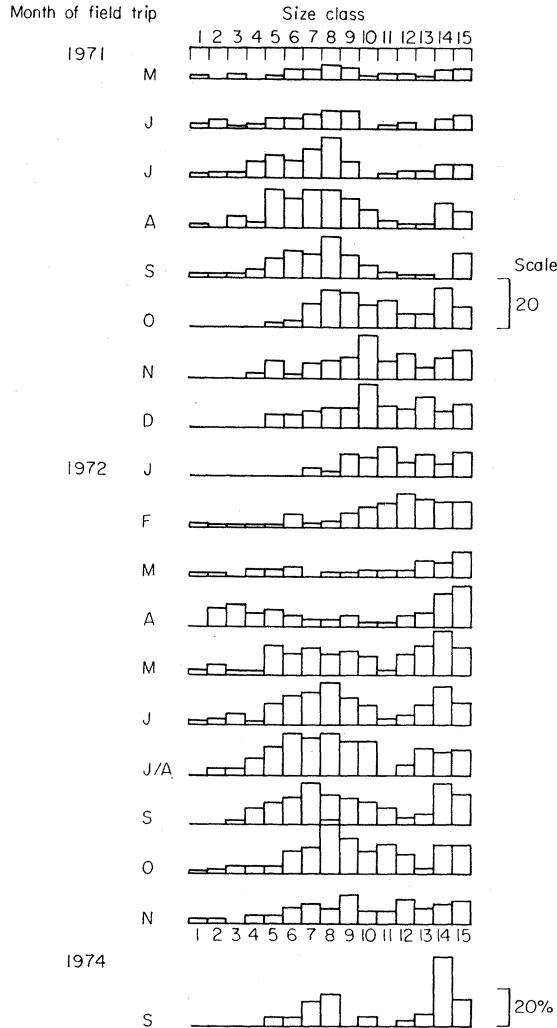


FIG. 4. The size class distribution of all *Geolycosa godeffroyi* living in burrows on the field site from May 1971 to November 1972 and in September 1974. The 1974 data are expressed as a percentage of the sample ($n = 89$) and the remaining data as the number of spiders.

were used to estimate the number of spiders passing through any size class in the interval between successive field trips. The number of spiders in any size class was plotted against time and integrated to produce an estimate of spider-days. The number of spider-days

divided by the duration of the size class in that season estimates the number of spiders passing through the size class (cf. Winberg 1971). These estimates are summarized in the right-hand column of Table 10.

Mortality

Laboratory studies were undertaken to assess the impact of mortality before the spiderlings gained the mother's back. Twelve egg sacs were collected from the field after they had expanded to make space for the hatching young (cf. Edgar 1968, Fig. 1.8). Egg sacs collected at this late stage could be expected to have the maximum degree of parasitism. They were maintained with the females under semi-natural conditions in artificial burrows and permitted access to a gradient of soil-water and to radiant heat for egg sac incubation

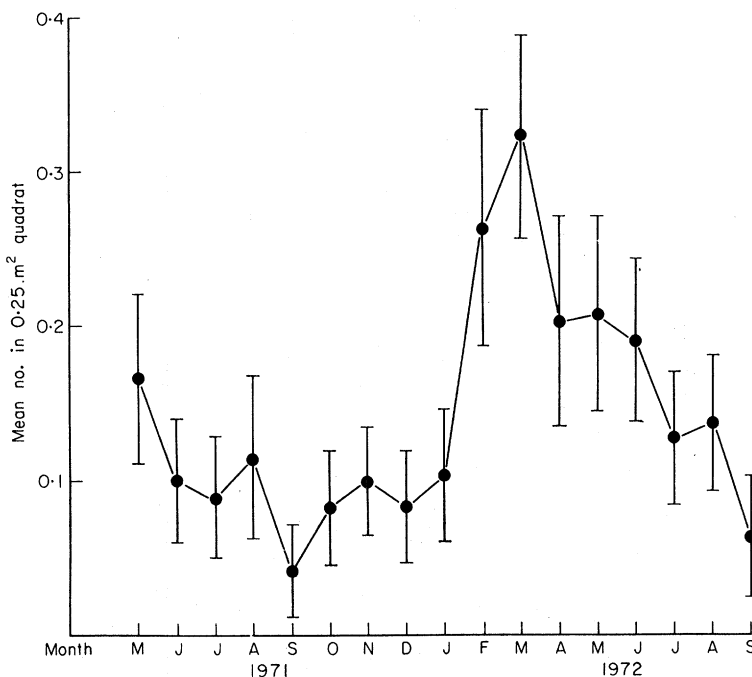


FIG. 5. The mean number of *Geolycosa godeffroyi* recorded in quadrats. The vertical bars represent \pm one standard error.

(Humphreys 1974). The females could therefore maintain their egg sacs at the preferred temperature and humidity. After the spiderlings had gained the back of the females the discarded egg sacs were examined and the spiderlings counted. An average of 2.7% (range 0–28%) of the eggs had been parasitized by scelionid hymenoptera (undescribed genus) and 5.1% (range 0.4–7.4%) of the eggs died or the spiders failed to eclose successfully. Hence 7.8% of the eggs estimated to be in any egg sac were considered to have died in the field before reaching the spiderling stage. These figures are in general agreement with those from other lycosids in which, in the absence of parasitism, most of the eggs laid produced spiderlings (Hackman 1957; Edgar 1971b). The larvae of the dipteran parasites, *Ogcodes basalis* (Walk.) and *Pterodonitia melli* Erich. (Acroceridae), occasionally emerged from *Geolycosa godeffroyi* in the laboratory. The parasites destroyed the internal tissues

Table 10. *Estimated number of Geolycosa godeffroyi on the Kowan field site at each field trip from September 1971 to October 1972*

Size class	October 1972												Estimated no. passing through size class		
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July/Aug.	Sept.		Oct.	
1				177	313	813	236	334	369	156	68				5852
2						370	941	174	225	315	104	1	1	1	2088
3	112				148		313	259	149	160	137	1	2	2	1522
4	3	177	2		1		158	167	149	84	74	89	86	86	682
5	8	91	84	5	1	1	2	89	160	165	112	90	87	497	
6	7	180	77	93	4	4	3	87	83	168	216	92	98	953	
7	119	10	232	184	74	74	78	2	11	13	114	100	94	816	
8	13	16	7	8	1	1	1	2	8	17	15	17	16	60.1	
9	6	15	8	8	9	5	1	3	9	11	15	10	13	99.0	
10	10	9	17	18	8	7	2	1	7	8	10	9	8	101.6	
11	7	11	7	9	12	9	2	1	1	2	4	6	11	79.2	
12	3	6	10	8	5	13	2	4	8	3	1	2	8	28.5	
13	5	6	4	12	9	11	6	5	12	7	6	4	1	37.0	
14	6	17	12	7	5	10	6	13	17	15	13	16	15	16.4	
15	10	9	13	10	10	10	10	16	11	9	11	12	10	12.7	

of the host and emerged to pupate. The emergence figures were striking in the consistency of both the time of emergence and of the size class of the host. Throughout the study of *G. godeffroyi* there were normally at least fifty spiders in the laboratory but the only records of acrocerid emergence were from size classes 11 and 12 in February and March of both 1971 and 1972. These size classes were considered as the susceptible part of the population and the percentage of these size classes parasitised is given in Table 11.

Mortality was estimated for the period from October 1971–October 1972 from the three year classes present. The upper point was taken as the number of spiderlings (7446) estimated to reach the back of the females (size class 0 in Fig. 6). The other points are the sum of the estimates of the number of spiders passing through any one size class over the period considered (see Table 10). The mortality estimate is similar in nature to that used by Wiegert (1965) except that it includes the effect of the duration of the size classes on the population estimates. In Fig. 6 the upper line represents the estimated size class specific mortality and the lower line the age specific mortality estimated from the duration of the size-classes. The former is adequately described by the equation

$$\log y = 3.770 - 0.181 x; \text{ S.E. } b = 0.013, r = 0.97$$

where y = the number of spiders passing through a size class and x = the size class.

Table 11. *The numbers of Geolycosa godeffroyi of size classes 11 and 12 in the laboratory during February and March and the numbers of acrocerids emerging*

Year	No. in size classes 11 and 12	No. of acrocerids emerging		Spiders parasitized (%)
		<i>Pterodontia melli</i>	<i>Ogcodes basalis</i>	
1971	19	2	4 (+1)*	31.6
1972	31	5	7	38.7
Both	50	7	11	35.2

* Two emerged from one host.

The use of pooled data from more than one cohort, none of which was followed through its full cycle, is a suspect procedure. More confidence can be placed on such estimates if they are supported by similar estimates from successive years. For *G. godeffroyi* the period from May to September in successive years may be compared (Fig. 7) and the general form of the curves is similar in 1971 and 1972. In addition the actual number of spiders in burrows (size classes 8–15) and the estimated number of juveniles in size classes 1–7 were similar at the start and end of the period used in the mortality derivation (Table 12).

Considering only the actual number of spiders recorded, to the exclusion of those size classes (1–7) for which only estimates are available, a test on the distribution and numbers in October 1971 and October 1972 shows no difference ($\chi^2 = 5.558$ with 7 D.F., $0.9 > P > 0.5$). The population dynamics resulted in a stationary size class distribution in the upper eight size classes.

The nature of the regression, relating the numbers passing through each size class to the size class, implies a fairly constant size class specific mortality of 34.1% (Type III survivorship curve, Slobodkin 1962). The major upswing in the relationship at size classes 6 and 7 is not thought significant as there are few data represented in this region.

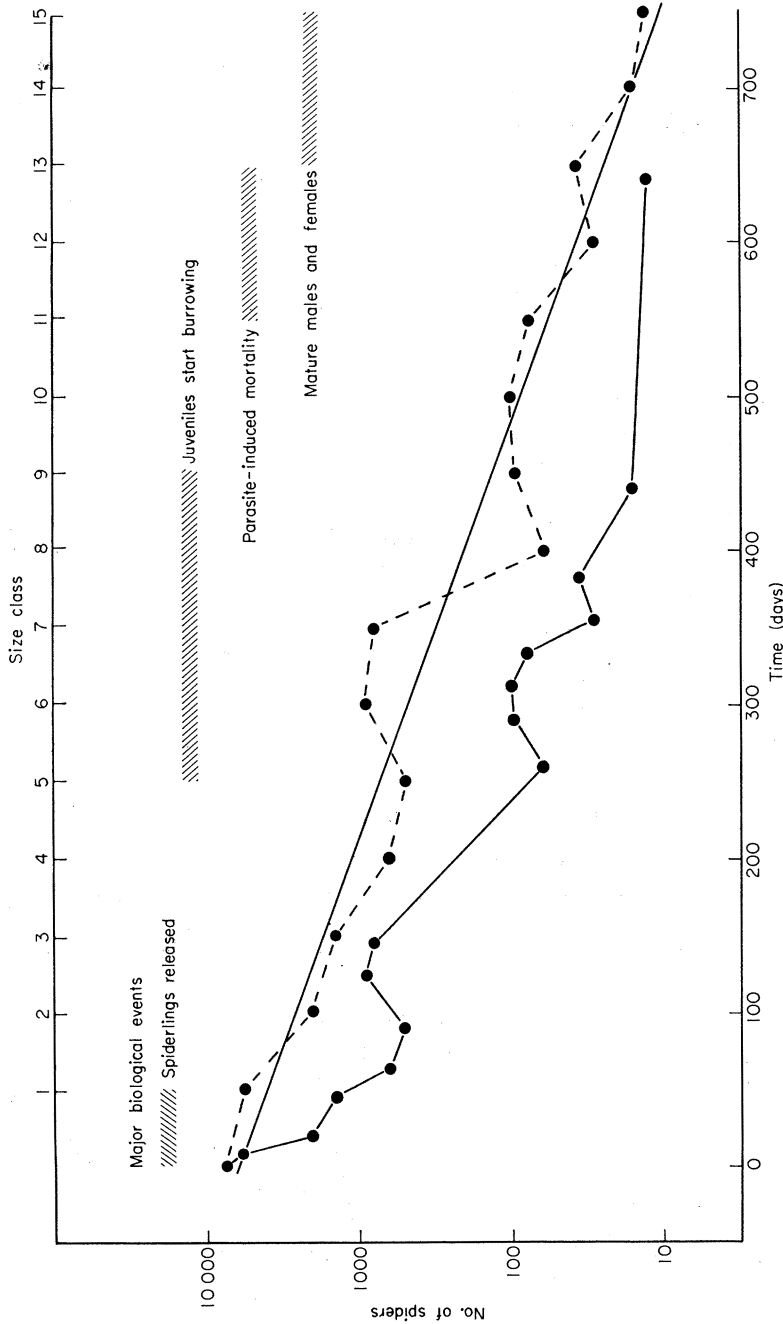


FIG. 6. The estimated size class specific and time specific mortalities of *Geolycosa godeffroyi* from October 1971 to October 1972. The upper curve represents the size class specific mortality and a regression line is drawn through the data. The lower curve represents the time-specific mortality. Note that the two curves do not coincide due to the variation in the duration of the size classes according to both the size class and the season. The biological events correspond only with the size classes.

The origin of the line is well fixed by the estimate of egg numbers derived from the weights of the egg sacs on the field site. The drop in the curve between size classes 11 and 13 coincides with the size classes in which the laboratory estimates indicated that there could be a 39% parasite induced mortality in 1972 (Table 11). In the field there was an estimated 64% drop in the number passing through this size class. The sum of the estimated parasite-induced mortality and the general trend in mortality is 73%, which is similar in magnitude to that found in the field.

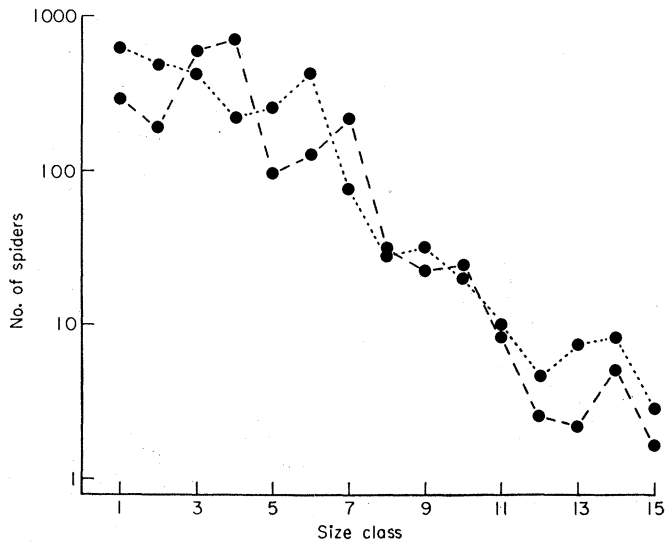


FIG. 7. Comparison of the estimated number of spiders passing through each size class during the period May–September 1971 (—●—) and the same period in 1972 (····●····).

Table 12. *The number of Geolycosa godeffroyi on the Kowan field site in October 1971 and October 1972; size classes 1–7 estimated from quadrats and size classes 8–15 equals number captured or seen*

Year	Size class									
	1–7	8	9	10	11	12	13	14	15	
1971	442	16	15	9	11	6	6	17	9	
1972	474	16	13	8	11	8	1	15	10	

The numbers passing through size classes 13 and 14 were estimated at 37 and 16.4 respectively. Assuming that the general trend in mortality (34%) applies to these size classes, then 66% of those present in size class 13 should have reached size class 14, i.e. 24.4 spiders. However, most males reach maturity at size class 14 and are effectively lost from the population as they become peripatetic. Assuming a 1:1 sex ratio, as found elsewhere, then $(37/2) \times 0.66 = 12.2$ spiders should have been recorded passing through size class 14 compared with the estimated 16.4. However, the estimated number of spiders in size class 14 includes the capture of males on thirteen occasions and this added 2.2 to the estimated number of spiders passing through this size class. This must be subtracted from 16.4 giving 14.2 to make it comparable to the 12.2 spiders that would theoretically have

passed through size class 14 assuming a 1:1 sex ratio and the model mortality schedule. This agreement indicates that the interpretation of the biology and dynamics of these size classes is realistic.

The general constancy of the estimated size class specific mortality was unexpected; I had assumed that mortality would have been considerably reduced after the spiders started burrowing. However, the mortality schedule is similar to those derived for other, more vagrant, spiders.

DISCUSSION

The phenology described is in general agreement with other work on lycosids. In Scotland *Pardosa lugubris* Walck. overwinters twice (Edgar 1971a) but in Holland may be able to reach maturity after only one winter (Edgar 1972). *Lycosa T-insignita* Boes et Str. in Japan and *Pardosa monticola* Clerck, *P. nigriceps* Thorell and *P. pullata* Clerck in the Netherlands overwinter once (Miyashita 1969; Vlijm & Kessler-Geschiere 1967). In California *Tarentula kochi* overwinters twice (Hagstrum 1970, 1971). All these species are small compared with *Geolycosa godeffroyi*. *Lycosa carolinensis*, which in size and habits is similar to *Geolycosa godeffroyi*, was considered to reach maturity by the second winter, when the males died, and to breed the following summer (Kaston 1948, p. 323). The rapid development rate in *G. godeffroyi* is facilitated by its habit of behavioural thermoregulation (Humphreys 1973, 1974) and high feeding rate (Humphreys 1975).

Hagstrum (1970) estimated fecundity and the number of adults and size classes 7 and 9 in a population of *Tarentula kochi*. He derived a model of mortality similar to that presented for *Geolycosa godeffroyi* with a constant mortality of 22.3% per size class. He estimated fecundity from the number of males and assumed a 1:1 sex ratio and one egg sac per female. His estimates were based on from one to three estimates of the three size classes. This species produced an average of sixty eggs per cocoon compared with a mean of 338 by *G. godeffroyi*.

Breymeyer (1967) presented data for a laboratory population of *Trochosa ruricola* Deg. The mortality for the three size classes can be well defined by a logarithmic relationship similar to that presented for *Geolycosa godeffroyi*. The field data for the web-building spider *Sigma hamata* (Clerck) (Kajak 1967, Table 1) can be reasonably defined by a similar relationship, with a constant 50% mortality per 'stage'.

Edgar (1971b) presented a scheme of mortality for *Lycosa (Pardosa) lugubris*. He estimated 79.8% mortality between the spiderlings and the 'smaller instars' compared with the estimated 64.4% mortality between the spiderlings and the second size class in *Geolycosa godeffroyi*. Mortality in *Lycosa (Pardosa) lugubris* continued at about 30% per month until the spiders overwintered. In their second summer the juvenile mortality in *L. lugubris* dropped to 5% a month and increased to 16 and 24% in the sub-adults and adults respectively. He assumed that there was no mortality in winter, which could account for the high estimated mortality of the sub-adults. In *Geolycosa godeffroyi* the equivalent to Edgar's 'larger instars' may be taken as size classes 9-11, thus excluding those in which there was thought to be heavy parasite induced mortality. The mortality in these size classes was estimated to be 10.5% per size class or 15.3% per month. The general trends in the estimated mortality in these two species are similar.

Despite the differing levels of detail in the studies referred to above, all appear to yield a Type III (Slobodkin 1961) survivorship curve. This form of survivorship curve may be generally applicable to spiders and has been found for the scorpion *Urodacus yaschenkoi* (Shorthouse 1971).

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SUMMARY

(1) The life cycle and population structure of a burrow inhabiting wolf spider, *Geolycosa godeffroyi*, were examined in the Australian Capital Territory. The phenology of the life cycle was similar to that of the much smaller lycosid, *Lycosa (Pardosa) lugubris*, in Scotland. The females produced egg sacs in the summer and the young from these egg sacs over-wintered twice before maturity, about fifteen instars later. These females died by the end of the third winter.

(2) The burrowing habit of the spiders enabled the field determination of growth rates and of fecundity. The females produced an average of 1.8 cocoons, each containing an average of 338 eggs. About 7.8% of the eggs were estimated to die before the spiderling stage.

(3) Two periods of parasite induced mortality occurred, the first in the eggs, caused by scelionid hymenoptera and the second at size classes 11 and 12, caused by acrocerid dipterans.

(4) The population was estimated using a combination of quadrat counts and trapping over a period of 599 days. No spiders were removed permanently from the population. The population was divided into fifteen size classes on the basis of the field-determined growth increment through the instars.

(5) A stationary age distribution was indicated in the population.

(6) The number of spiders passing through each size class was used to estimate the mortality of the spiders. The spiders had a fairly constant size class specific mortality of 34%. The general mortality schedule, although unexpected, was similar to those derived for other spiders and resulted in a Slobodkin Type III survivorship curve.

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