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The Influence of Burrowing and Thermoregulatory Behaviour on the Water Relations of *Geolycosa godeffroyi* (Araneae: Lycosidae), an Australian Wolf Spider

W. F. Humphreys

Department of Zoology, Australian National University, Canberra, A.C.T. 2600, and
Department of Zoology, La Trobe University, Bundoora, Vic. 3083

Summary. The water loss from the wolf spider *Geolycosa godeffroyi* (L. Koch) is presented for a wide range of environmental conditions. Water loss is influenced by the size of the spider, temperature, saturation deficit and by relative humidity *per se*. The spiders thermoregulatory behaviour more than doubled water loss. Water could not be extracted from near saturated air but was available from the soil when the soil water content was greater than 11%. Due to the spiders burrowing habits both the active and passive use of heat differentials were potential sources of free water.

Introduction

The importance of water availability to terrestrial arthropods is implied in the numerous studies of water loss. Rarely, however, do the experimental conditions used encompass the range of environmental conditions found in the field and it is frequently difficult to obtain field measurements of the appropriate microenvironment.

An opportunity to investigate the water relations of an organism is provided by a species whose life-system is centred on a burrow as this enables sufficiently detailed measurement of temperature and humidity over a period of time. Such an organism is provided by the burrow dwelling wolf spider *Geolycosa godeffroyi* (L. Koch). The choice of a spider is pertinent as no studies of water loss from spiders have included a realistic range of temperature and humidity or a complete range of life stages.

The habitat and population processes of *G. godeffroyi* have been described (Humphreys, in press) and long term recording of the internal body temperatures has shown that this species exhibits efficient behavioural thermoregulation throughout the year. It can maintain its body temperature above the ambient air temperature throughout 24 hrs by basking in the sun during the day and withdrawing down its burrow at night (Humphreys, 1974). In consequence the spiders grow rapidly (Humphreys, in press) and have a high feeding rate (Humphreys, 1975). The spiders inhabit burrows for all save the first few months of life. The burrows vary in depth, from 4–18 cm, depending on the size of the spider and the season (Humphreys, 1973). In this paper the microenvironment of the spiders is described and a model presented relating the appropriate physical variables to water loss. The ability of the spiders to obtain water is discussed.
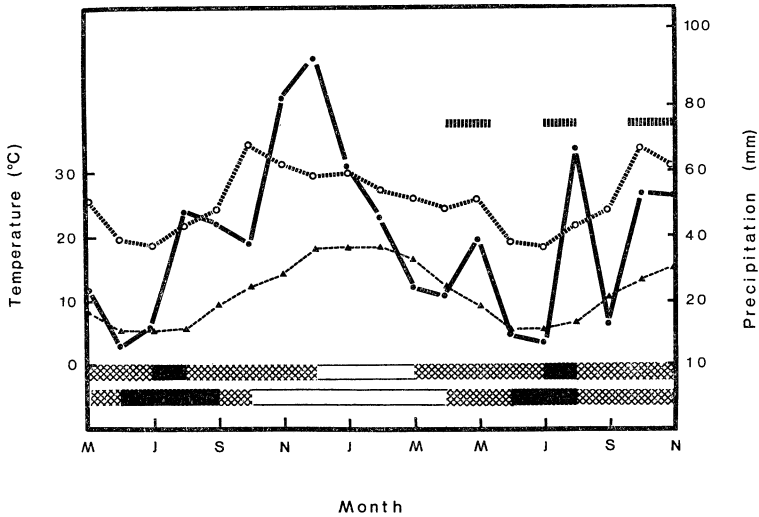
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Month

Fig. 1. Composite climatic [Walter and Lieth (1960) type] and synoptic diagram for Fairbairn
Meteorological Station, A.C.T. (Altitude 571 m, mean annual temperature 12.7° C, mean
annual precipitation 622 mm, years of observation 33) (absolute minimum temperature
−10.0° C, mean minimum of coldest month −0.4° C, absolute maximum temperature 42.4° C,
mean maximum temperature of hottest month 27.5° C). The synoptic records cover the
period from May 1971 through November 1972, and the climatic information is completed
for the 33 year mean values. The upper line (o) represents mean monthly precipitation and
the continuous line (•) the precipitation actually recorded over the time period represented
by the diagram. The lower broken line shows the mean daily temperature for each month
(the climatic mean temperatures were close to the synoptic means and are not illustrated).
Using a fixed relationship of 10° C to 20 mm precipitation unfavourable periods for plant
growth due to water shortage are indicated when the precipitation curve falls below the
temperature curve. Thus on a climatic basis water shortage does not occur but from the
synoptic records for the period covered by the study, water shortage was indicated in June
1971 and in March, April, June, July and September of 1972. The heavy broken lines at
the upper right of the figure show the periods during which field and laboratory studies
indicated that soil-water was unavailable to *G. godeffroyi* on the Kowan field site. This is
discussed in the text. The heavily hatched bars at the foot of the diagram represent the period
during which the mean minimum temperature was less than 0° C and the lightly hatched
bars the period when the absolute minimum temperature was below 0° C. The upper and
lower bars represent the climatic and synoptic records, respectively

    Climate. The Kowan field site was situated 6.8 km from the Fairbairn Meteoro-
logical Station at an altitude of 620 m in the Australian Capital Territory. The
area is characterised by unreliable moderate rainfall, high summer temperatures
and frost which may occur in up to 9 months of the year. Synoptic information
for the Fairbairn Meteorological Station is shown in Fig. 1 for the period in
which the field work for this study was conducted. The winter of 1971 was the
most severe on record and drought conditions existed through much of 1972.
    Microenvironment. Steep gradients of temperature and humidity are found
in most environments (Wellington, 1960; Nørgaard, 1951; Williams, 1954;
Cloudsley-Thompson, 1962; Holm and Edney, 1973) and mobile organisms are
subjected to rapid and frequently severe changes in their physical surroundings.

If the validity of using standard meteorological measurements cannot be established there is no alternative to making detailed microenvironmental measurements (Cloudsley-Thompson, 1962). Bursell (1964a), in concluding a discussion on this subject, thought that it may be advisable to take measurements from the animal itself and that "to assess the conditions to which insects are exposed, one would need to have a rough idea of the proportion of time spend in different types of activity and the places frequented at different times of the day and night, as well as any seasonal variations in these respects". Macfadyen (1967) cautions that it is frequently necessary to forgo accuracy for realism.

Methods

Spider Temperature. Spider temperature were measured continuously for 24 hr periods using implanted thermocouples (Humphreys, 1973, 1974). Data were obtained for 26 days throughout 1972.

Ambient Temperature and Humidity. Standard humidity measurements were made about every hour in the field except for about 6 hrs at night. Interpolation during this period was made with the aid of a meteorological thermohygrograph in a Stevenson's screen placed at ground level and with the responsive elements 10 cm above the ground. The standard measurements were made with a psychrometer (Psychron model 566; Bendex Corporation, Baltimore) laid in the ground so that the 1 cm deep inlet sampled air from the surface.

Burrow Humidity. Burrow humidity was investigated using cobalt thiocyanate papers according to the directions in Solomon (1957). The papers were placed in small perforated polythene vials, to prevent contamination, and lowered into the burrows to known depths.

Soil Water. Electrical resistance (Bouyoucos) blocks (Bouyoucos and Mick, 1940, 1947; Bouyoucos, 1954; Sterling *et al.*, 1961) were used to measure soil water.

Two types of electrode were calibrated and installed in the field. Type One were commercially obtained parallel wire electrodes and Type Two were parallel screen electrodes constructed according to the directions in Sterling *et al.* (1961, p. 52). The electrodes were calibrated in closed containers of soil from the Kowan field site over the range of 0% to 30% (w/v) soil-water. A commercial circuit testing meter was used both for the calibration and field measurements.

The blocks were located around the field site at 3, 6, 12 and 19 cm depth taking appropriate precautions on installation (Sterling *et al.*, 1961). Following a one month equilibration period readings were taken weekly in both directions to prevent polarisation of the electrodes. Only the Type Two electrodes remained in good repair and recalibration of these showed that drift had been negligible in the electrodes recovered.

Transpirational Water Loss. Short term weight loss in starved insects can be attributed to water loss provided no excretion occurs (Gunn, 1933; Rapoport and Tschapek, 1967). It is difficult to define the conditions in water loss experiments conducted in still air (Ramsay, 1935) so the moving air method of Edney (1951) was adopted which permitted the control of temperature and humidity of the air moving at 0.72 cm sec^{-1} over a number of animals.

Air was conditioned by passing it through flasks containing sulphuric acid of the required specific gravity (Wilson, 1921; Solomon, 1951). The air passed through the experimental chamber following passage through a heat exchange coil and a filter to remove acid aerosol. The whole apparatus was immersed in a water bath at the experimental temperature. Spiders used in the experiments were adapted at the experimental temperature for 7–10 days at 60–80% R.H. and were provided with water but not fed. All weighing was performed on either a Mettler balance to 0.1 mg or a Cahn electro-balance to an accuracy appropriate to the weight of the spider.

Preliminary experiments showed that weight loss was higher in the first than in subsequent hours, probably due to water adsorbed onto the cuticle (Loveridge, 1968a). Spiders were therefore pretreated in the apparatus for 1 hr before the initial weighing and then left in the apparatus for 24 hrs and reweighed. Spiders which defaecated or ecdysed were exluded from the results. The weight loss was initially expressed as weight loss per individual per hour. Experiments were run over as complete a size range of spiders available un-

Table 1. Combinations of temperature and relative humidity used in the water loss experiments
to obtain ten saturation deficits

Temperature (° C)	Relative humidity (%)	Saturation deficit[a] (g m^{-3})
5	30	4.76
5	80	1.36
15	30	8.98
15	80	2.57
25	30	15.25
25	80	4.36
35	30	27.70
35	80	7.93
45	30	45.85
45	80	13.10

[a] Saturation deficits are calculated at 1 standard atmosphere of 1013.25 mb. For ranges of environmental conditions from 700 mb to 1100 mb, −20° C to 50° C and 0% R.H. to 100% R.H. the compressibility factor given by List (1968) ranges from 0.9992 to 0.9999 and is ignored here.

der each experimental condition, normally about 1–1500 mg. The ten experimental conditions were produced by a combination of two relative humidities at each of five temperatures (Table 1).

Water Uptake from Humid Air. Following the method of Lees (1946), *G. godeffroyi* were tested to determine whether they could make any substantial contribution to their water balance by absorbing water from near saturated air. The spiders were deprived of water for 3 days and then placed in an atmosphere of 92% or 98% relative humidity, obtained over saturated salt solutions (Wilson and Bates, 1960).

Water Uptake from Soil. To relate the soil water profiles obtained from the field site to the spiders it was necessary to determine the level at which soil water became available to the spiders. This type of experiment is difficult to control because the saturation deficit varies over soils of differing water content. The experiment was designed so that each experimental spider had an individual control spider within 3% of its own weight. The spiders varied in weight from about 100 mg to 1400 mg. Three experimental and three control spiders were used under each condition of soil water. The spiders were individually placed in containers with 100 g of soil from the field site which had been conditioned for 1 week at the appropriate soil water content. The experimental spiders were placed on a single layer of netting, to stop them burrowing and to prevent contamination by soil or free water, but through which they could reach the soil. The control spiders were placed on a double layer of netting which prevented the spiders from reaching the soil. Both the experimental and control spiders were thus subjected to similar saturation deficits.

The spiders were deprived of water for 3 days at 20° C and 60–70% R.H. and then placed in the containers. The change in weight was measured at intervals, and after 55 hrs the control spiders were allowed the same access to the soil as the experimental spiders.

Results and Discussion

Ambient Environment

The sensitivity of the method for sampling the surface air was examined by running a series of humidity profiles above the ground (Fig. 2). Large changes in humidity were recorded by raising the inlet only 0.5 cm and the instrument was considered to sample a reasonably consistent and restricted surface layer. These humidity profiles and their diurnal variation were similar in magnitude
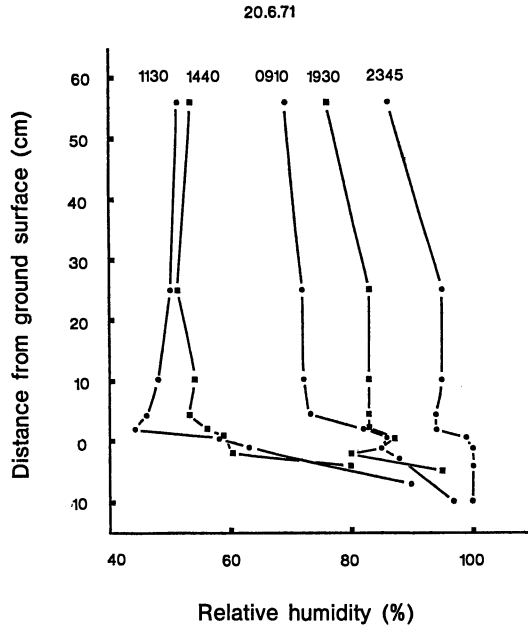
20.6.71

Fig. 2. Gradients of relative humidity away from the ground surface throughout the day on 20. 6. 71. Points above the surface represent the air relative humidity and points below the surface the humidity in the larger burrows of *G. godeffroyi*

and temporal changes to those found in Finland using more sophisticated instrumentation (Huhta, 1971).

Some results of the determination of burrow humidity for the same day as the air profiles are included in Fig. 2. Determinations at the different times each represent a different similarly sized burrow. The top few cm of the burrow had a similar humidity to the ground surface throughout the day but there were steep gradients in humidity below this level during the day. At night the surface humidity approximated the deep burrow humidity and this general pattern was repeated throughout the year. Air spaces in soil are saturated with water at all times save during periods of severe drought (Rapoport and Tschapek, 1967). The air in the smaller burrows could thus be expected to be close to saturation most of the time, except near the opening.

These general patterns permitted a simplified monitoring of the humidity environment of the spiders. The rationale underlying the method is as follows. During the day when the spiders exhibited behavioural thermoregulation (Humphreys, 1974) they spent most of the time close to or at the mouth of the burrow and were exposed to humidities close to those recorded at the ground surface. At night the spiders were either in the depth of the burrow or at the surface, depending on the ambient temperatures (Humphreys, 1973). The ambient surface humidity rose rapidly at dusk and generally remained high throughout the night. The differential between the deep burrow humidity and the surface humidity at night would never be extreme. The difference between the 10 cm screen
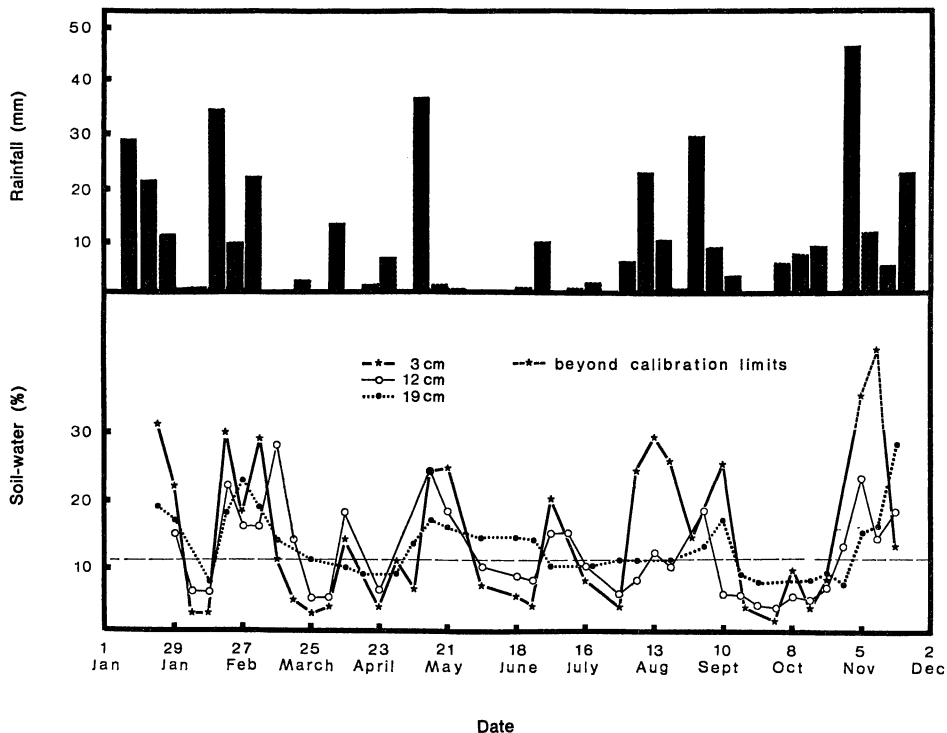
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Fig. 3. Records of weekly rainfall at Fairbairn and soil water content at three depths at Kowan throughout 1972. The fine line at 11% soil water content is the level below which soil water is unavailable to the spiders (see Discussion)

humidity and the surface humidity was small at night and the former records were used to interpolate the humidity records at night when no surface records were available.

Soil Water

The results obtained from three depths are illustrated in Fig. 3 together with the weekly rainfall figures from Fairbairn Meteorological Station. The soil-water profiles had many of the characteristics of the thermal profiles found in the soil. There was a gradient of water with depth and the amplitude of the fluctuations was reduced away from the surface. The periodicity was controlled by the input of rain at the surface and the evaporation and drainage characteristics of the soil. A small fall of rain between June 18 and July 16 markedly affected the soil-water at 3 cm but had little effect at 19 cm. The rise in soil-water at 19 cm lagged behind that at 3 cm and had a smaller amplitude as seen on February 27, September 10 and during November. In March and June there were periods when the deep water content was high while the upper level was dry. The converse situation occurred in November. It is apparent that the spiders had access to a range of soil-water content due to their inhabiting burrows. The relevance of this will become apparent later.

Transpirational Water Loss

Effect of Sex on Water Loss. Only the final two instars could be differentiated according to sex. As the males were only seasonally represented in collections for the laboratory, few of the experimental conditions contained sufficient males to examine the influence of sex. The data from sex determined spiders were expressed as a weight specific rate, analysed for homogeneity and the means compared using a *t*-test for unequal sample size (Sokal and Rohlf, 1969, p. 221). No significant differences were found in the rate of water loss between the sexes (Table 2) and in further treatment of the results sex differences were ignored.

Effect of Weight on Water Loss. Initial examination of the results showed that there was a curvilinear relationship between the weight of the spiders and water loss. The results were reexamined after double logarithmic transformation to produce a straight line relationship more suitable for analysis. The resulting regression equations are presented in Table 3. All the regressions are significant ($P<0.001$) but there is heterogeneity between the data for the different condi-

Table 2. Comparison of water loss from male and female *Geolycosa godeffroyi*

Experimental condition		Water loss (mg g^{-1} hr^{-1})									
Temp. (° C)	R.H. (%)	Males			Females			Statistic			
		Mean	Variance	N	Mean	Variance	N	F	t_s	D.F.	P
25	30	2.89	1.130	13	2.42	1.062	15	1.06	1.19	26	0.4–0.2
35	30	3.22	1.773	13	2.93	1.730	14	1.03	0.75	25	0.5–0.4
35	80	2.16	0.944	6	2.37	0.345	9	2.74	0.53	13	0.9–0.5
45	30	17.18	4.870	9	15.71	13.870	17	2.85	1.08	24	0.4–0.2

Table 3. Regression parameters describing the relationship between water loss from *Geolycosa godeffroyi* ($\log_{10} Y$ mg hr^{-1}) and the spider weight ($\log_{10} X$ mg) at two relative humidities at each of five temperatures

Temperature (° C)	Relative humidity (%)	N	Regression equation	Standard error		Correlation coefficient	t_s	P
				a	b			
5	30	28	$Y = 0.675\,X - 2.449$	0.157	0.074	0.872	9.09	<0.001
5	80	32	$Y = 0.763\,X - 2.580$	0.141	0.066	0.905	11.63	<0.001
15	30	28	$Y = 0.930\,X - 2.647$	0.091	0.037	0.980	24.87	<0.001
15	80	21	$Y = 0.883\,X - 2.629$	0.118	0.052	0.969	17.04	<0.001
25	30	71	$Y = 0.931\,X - 2.407$	0.071	0.029	0.968	32.08	<0.001
25	80	45	$Y = 0.762\,X - 2.330$	0.121	0.057	0.899	13.43	<0.001
35	30	72	$Y = 0.787\,X - 2.001$	0.070	0.030	0.954	26.56	<0.001
35	80	37	$Y = 0.861\,X - 2.275$	0.128	0.051	0.944	16.93	<0.001
45	30	51	$Y = 0.938\,X - 1.593$	0.061	0.023	0.985	39.57	<0.001
45	80	27	$Y = 0.915\,X - 1.854$	0.076	0.034	0.984	27.18	<0.001

Bartlett's test for residual variance on all the data; $\chi^2 = 51.9$ with 9 D.F., $P < 0.001$.

tions (χ^2=51.9, P<0.001) which cannot be attributed to any few experimental conditions. This may result from the different preconditioning of the spiders as found by Loveridge (1968a, b) for *Locusta*.

The slopes (b) of the regressions are positive and less than 1.0, where b is the power function in the equation $y=ax^b$. It follows that spiders lost absolutely more water as they became larger but did so at a decreasing weight specific rate. The mean power function of 0.85 indicates that water loss is not directly related to either the weight (b=1.0) or surface area (b=0.67) of the spiders.

Derivation of Water Loss Model. From the experimental results a model can be derived to relate water loss to the environmental conditions and spider weight. Multiple regression analysis was considered the most appropriate for the type of data available. The data from the water loss experiments cannot strictly be pooled due to its heterogeneity. Moderate heterogeneity in itself is not too serious but single degree of freedom comparisons may be far from accurate (Sokal and Rohlf, 1969, p. 376). Given the large number of degrees of freedom in this analysis the overall tests of significance would be reliable enough to allow best use of transformations of the data. Furthermore a model is a predictive tool and does not necessarily require a statistical basis.

The multiple regression was used to predict water loss from the spider weight, saturation deficit and temperature and yielded the equation presented in Table 4 which accounts for 92% of the variance in the data.

Processes of Water Loss. After eliminating the data causing the heterogeneity and analysing the remaining data the resulting multiple regression model was similar and had similar confidence limits to that derived from the complete data. The confidence limits resulting from the analysis of the complete data are therefore considered to be approximate but realistic. An initial analysis was therefore undertaken on the entire data to separate the importance of temperature and saturation deficit to water loss. The partial correlation coefficients (Snedecor, 1956, p. 401) resulting from an analysis of the correlation matrix in Table 4 gave r (YX_3X_2=0.210), indicating that saturation deficit and temperature were of similar importance to the measured water loss. A more detailed examination of the data however reveals that the effects of temperature and humidity on water loss are not simple.

The most convincing way of demonstrating the effect of temperature *per se* on water loss is to compare the water loss at similar saturation deficits but different temperatures. Three pairs of regressions can be treated in this way (Table 5). An analysis of variance indicates that each pair of lines are parallel but displaced except in the first comparison which is suspect due to the significant Bartlett test (P<0.005). In all comparisons the higher temperature had a greater water loss despite a slightly lower saturation deficit. The latter would tend to decrease the separation of the lines. There was a critical temperature above which water loss markedly increased but water loss was affected by temperature even below this critical temperature.

When the mean weight specific rate of water loss was plotted against both saturation deficit and temperature it showed that there was a temperature above which the rate of water loss markedly increased (Fig. 4a). The transition is similar to that found for other spiders (Davies and Edney, 1952) and indicates

Table 4. Multiple regression model relating water loss (Y mg hr^{-1}) to the live weight of the spiders (X_1 mg), temperature (X_2 °C) and saturation deficit (X_3 g m^{-3})

Form of the equation:

$$\log_{10} Y = \log_{10} X_1 b_1 + X_2 b_2 + X_3 b_3 + b_0,$$

where;

		S.E.	t
$b_0 =$	-2.967		
$b_1 =$	0.861	0.0148	58.15
$b_2 =$	0.0187	0.00149	12.51
$b_3 =$	0.0129	0.00138	9.336
$n =$	410		
$R^2 =$	0.921		

Analysis of variance:

	D.F.	M.S.	F	
Regression	3	108.42	1569.0	$P < 0.001$
Residual	406	0.0691		

Correlation table:

408 D.F.

Y	1.0			
X_1	0.862	1.0		
X_2	0.475	0.088	1.0	
X_3	0.475	0.109	0.738	1.0

Table 5. Comparison of the regression lines relating water loss from *G. godeffroyi* to the spider weight. The data obtained from experiments with similar saturation deficits are compared

Environmental conditions compared			Bartlett's χ^2 test for residual variance			Test of parallelism			Test of identity		
Temperature (°C)	Relative humidity (%)	Saturation deficit (g m^{-3})	D.F.	χ^2	P	D.F.	F	P	D.F.	F	P
5	30	4.76									
25	80	4.36	1	9.75[a]	<0.005	1, 68	0.01	>0.75	2, 68	9.98[a]	<0.001
15	30	8.98									
35	80	7.93	1	1.37	0.5–0.1	1, 61	1.17	0.5–0.25	2, 61	12.31[a]	<0.001
25	30	15.25									
45	80	13.10	1	0.70	0.9–0.5	1, 93	0.14	0.75–0.5	2, 93	56.17[a]	<0.001

[a] Denotes significant test.

that a waterproofing layer broke down at higher temperatures. The figure shows that the transition in the water loss curve was dependent on the temperature rather than the saturation deficit. As the spiders reached temperatures of about

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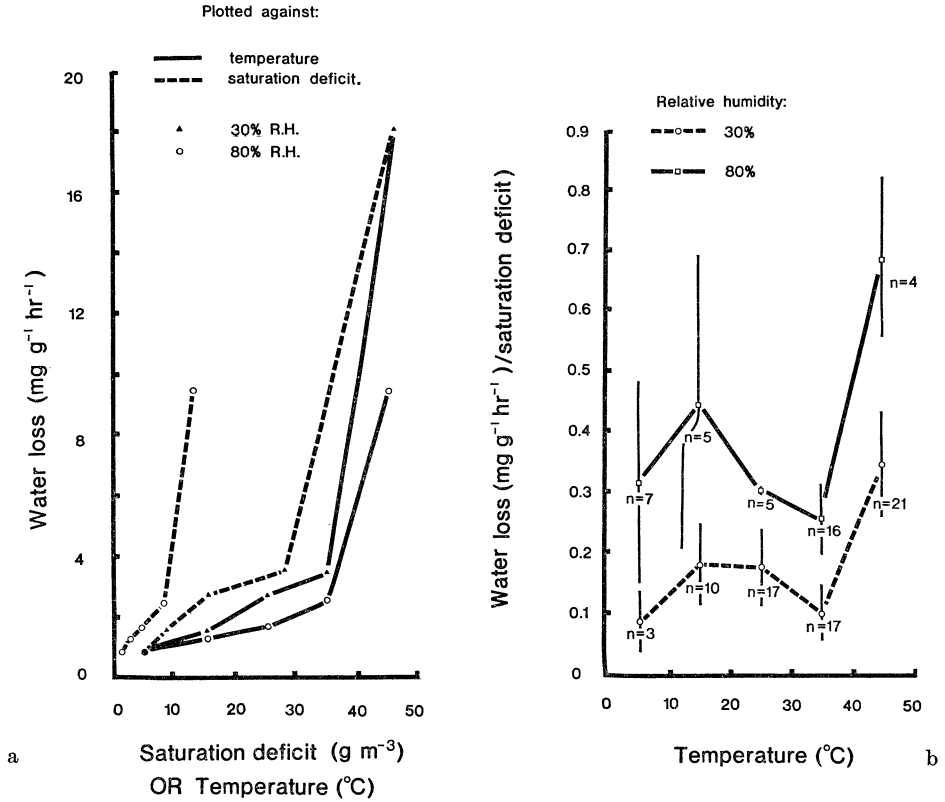
Fig. 4. (a) Mean rate of water loss from all spiders under each of ten experimental conditions. The means are plotted against both saturation deficit and temperature showing that the sudden increase in water loss is related to temperature rather than saturation deficit. (b) The effect of temperature and relative humidity on the rate of water loss after the effect of saturation deficit has been excluded. The mean rate of spiders greater than 800 mg from each of two conditions of relative humidity have been joined. The vertical bars represent $\pm$ one standard deviation

$40°$ C in the field the transition temperature was probably between 40 and $45°$ C, compared with a transition temperature of $42°$ C in *L. amentata* (Davies and Edney, 1952).

The effect of saturation deficit can be excluded by dividing the weight specific rate of water loss by the saturation deficit (Beaument, 1958; Loveridge, 1968a). The technique was applied to all individuals of *G. godeffroyi* greater than 800 mg in weight (Fig. 4 b) and further illustrates the relationship between water loss and environmental conditions. In all cases the greater water loss occurred at the higher relative humidity and this was partially independent of the saturation deficit. There was heterogeneity in the data below $35°$ C but the difference between the means was significant at $35°$ C ($t=2.051$, $0.05>P>0.02$) and $45°$ C ($t=6.592$, $P<0.001$). This suggests that relative humidity *per se* had an effect on a mechanism for the control of water loss.

The indications are that the processes involved in water loss were similar to those described for *Locusta* by Loveridge (1968a, b). Loveridge considered that water loss through the cuticle of *Locusta* was proportional to the weight of the animal. His results clearly show that it was not proportional to, but linearly related to the weight. Loveridge (1968b) showed that water loss was apparently controlled to some extent at high saturation deficits and went on to show (Loveridge, 1968a) that this anomalous relationship was caused by a reduction in the permeability of the cuticle occurring at low relative humidities. Whole body loss was also less than expected at low humidities and probably (1968b) resulted from active measures to control water loss from the tracheal system by a combination of spiracular and ventilatory movements. The results for *G. godeffroyi* support Loveridge's findings and indicate that the mechanisms involved in the control of water loss from arthropods are more complex than generally accepted.

Spiders may force ventilate their lung-books (Berridge, 1970) and this process may be connected with the control exerted by the spiracles over the movement of air. *Lycosa amentata* (Clerk) lost 50% more water when maintained in an atmosphere of 10% carbon dioxide compared with control spiders in normal air (Davies and Edney, 1952). High concentrations of carbon dioxide cause the spiracles to remain open. The release of carbon dioxide from *G. godeffroyi*, as recorded on an infra-red analyser, showed a marked periodicity in dry air but the periodicity was less conspicuous in moist air (Fig. 5). This indicates that spiracular control, probably coupled with forced ventilation, operated in *G. godeffroyi*, but neither was specifically demonstrated.

Although a simple linear regression model could be developed which accounted for most of the variance in the data relating water loss and the environmental parameters, water loss from *G. godeffroyi* obeyed none of the proposed laws governing water loss. Water loss was not a linear function of weight but an logarithmic function. Water loss was affected by relative humidity in addition to saturation deficit and temperature. *G. godeffroyi* had a number of potential methods of controlling the rate of water loss. Cuticular waxes were probably effective in reducing water loss at temperature sbelow 40° C and within the temperature range 5° C to 45° C the cuticle may respond to the relative humidity resulting in a reduction of water loss at low humidities. Alternatively low humidity may result in a change in the pattern of either spiracular control of the air movement into the lung-books or in the ventilatory pattern. Potential behavioural strategies are discussed later.

Comparison with Other Work. The literature contains no reports in which the water loss from spiders was examined over the range of variables used in the present study. The most comprehensive work is that of Davies and Edney (1952) but their results are difficult to compare with the present data as their experiments were short (15 min) and much of the reported water loss may have been the loss of water adsorbed onto the cuticle. Nørgaard (1945) found that several lycosids survived between 6 and 27 hrs at 20° C and 33% relative humidity except for *Pardosa* (*Lycosa*) *monticola*, which had a mean survival time greater than 48 hrs. None of the species of *Trochosa* tested by Engelhardt (1964; cited in Almquist, 1971) survived for 20 hrs at 25° C and 30% relative humidity. *G. godeffroyi* was clearly more resistant to desiccation than these European
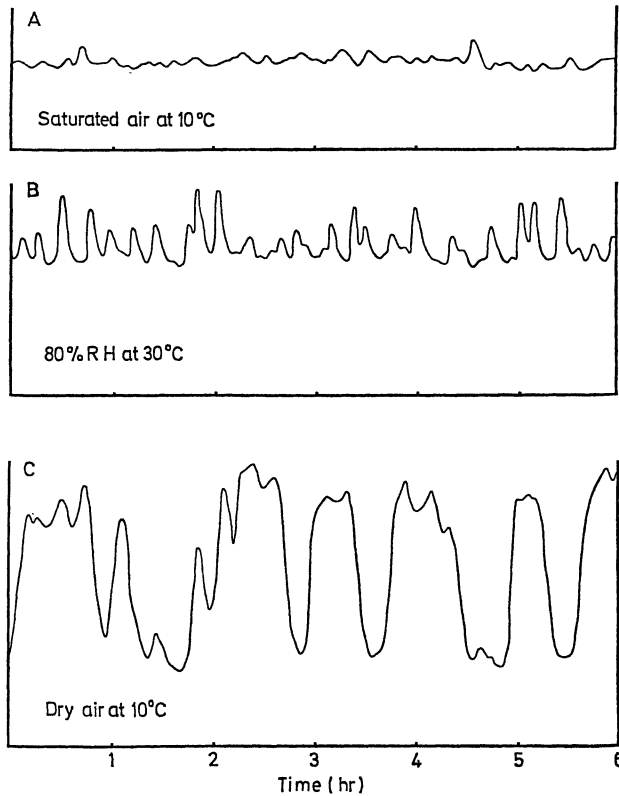
Fig. 5. Release of carbon dioxide from *G. godeffroyi* at different temperatures and relative humidities. Note the extreme periodicity of the release of carbon dioxide from spiders tested in dry air

lycosids because mortality was low under all experimental conditions even though the experiments ran for 24 hrs.

It is of interest to compare the results with those for the arid land scorpion *Uradacus yaschenkoi* (Birula) studied by Shorthouse (1971) as the same apparatus was used and some of the environmental conditions were identical. The rate of water loss in a 1 g scorpion at 35° C and 30% relative humidity was 2.05 mg hr^{-1}, when tested over 5 hrs (Shorthouse, 1971), compared with 2.29 mg hr^{-1} for a 1 g *G. godeffroyi*, tested over 24 hrs under the same conditions. The behaviour of the two species was in marked contrast. The scorpion minimised water loss by its nocturnal and burrowing habits while the spider enhanced water loss by basking in the sun. Despite this the resistance to water loss in the two species was similar and the different behavioural strategies adopted by them may partly reflect the availability of water in their environments.

Water Uptake

G. godeffroyi must replace the water lost to maintain its water balance within certain limits. Cribellate spiders of the genus *Ciniflo* Bl. died after losing 20% of their body weight through water loss (Cloudsley-Thompson, 1957) and similar

Fig. 6. The mean proportional weight change of spiders with access to soil of differing water content. Each point represents the mean proportional weight change of three experimental spiders with access to the soil minus the mean proportional weight change of three control spiders without access to the soil. Between 55 hrs and 58 hrs the control spiders we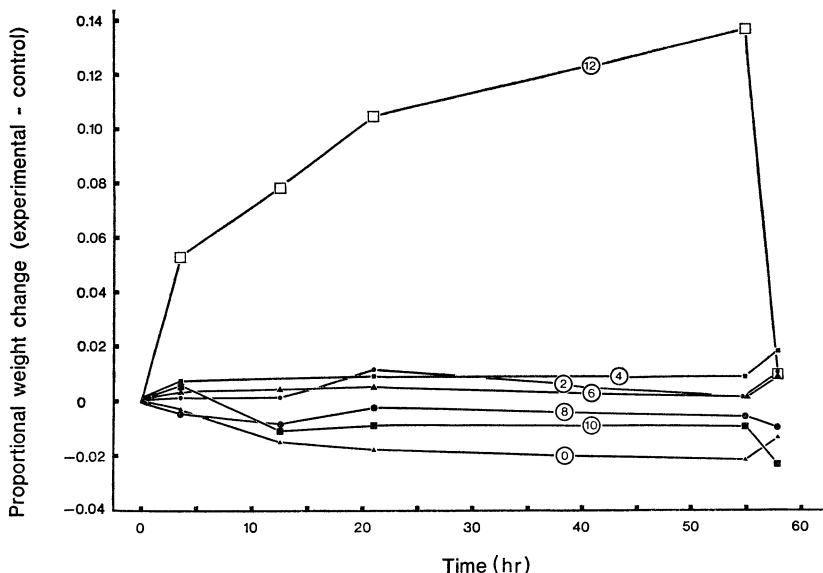re allowed access to the soil. The numbers in circles on the lines show the percentage soil water (w/v) to which the spiders had access

levels (26–31%) have been reported in Lagerspietz and Jäynäs (1958) for several families. In the water loss experiments, *G. godeffroyi* died after losing between 16% and 23% in weight but were incapacitated before they died. Insects tolerate about 15% weight loss before they die (Bursell, 1964b) which is similar to the level found for *G. godeffroyi* and this is taken as the critical value in further discussion.

From Near Saturated Air. Some arthropods can extract water from near saturated air and amongst the arachnids, ticks use this strategy most effectively (Lees, 1946). When *G. godeffroyi* were exposed to relative humidities of 92% and 98% at 20° C the eight spiders lost an average of 3.04% (range 2.37–3.67%) and 2.13% (range 1.99–2.25%) of their body weight respectively over 24 hrs. Despite having been deprived of water before the experiments they did not gain weight and it must be concluded that the spiders were unable to gain sufficient water from the air to maintain their water balance. Similar results have been recorded for *Linyphia montana* (Lagerspietz and Jäynäs, 1958).

From Soil. The results were expressed as the mean proportional change from the initial weight. In Fig. 6 the results are plotted as the difference between the mean proportional weight change of the experimental and the control spiders under each experimental condition. Only at 12% soil water did the experimental spiders greatly diverge from the control spiders and this divergence was lost after the controls had access to the soil. In further discussion 11% soil water is taken as the level above which the spiders could obtain water from the soil (see Parry, 1954). The scorpion, *Urodacus yaschenkoi* was able to gain water from

sand with as little as 4% soil-water (Shorthouse, 1971). Under the experimental conditions used, in which the scorpions had access to the sand, small weight changes could be ascribed to water adhering to the cuticle, and only at 7% soil-water did the gain in weight, reported by Shorthouse, continue for some time.

Application of the Water Loss Model to the Field

There are currently no methods available for obtaining information on the water balance of free-living animals in humid environments. Tritium methods are reliable in dry air but when there is significant humidity it is difficult to quantify the surface interchange of HTO and H_2O (Green, 1972).

In the absence of field methods, water loss determinations conducted in the laboratory must be used in combination with environmental records to estimate water loss in the field. In the present study, detailed records of the temperature and humidity conditions to which G. godeffroyi was subjected were available at intervals throughout the year on 26 days. In addition a satisfactory model was derived relating these environmental variables to the weight of, and the water loss from, the spiders.

Two problems arise when attempting to apply this information to the field. The first concerns the effect of wind speed on water loss. No satisfactory method was available to monitor microenvironmental wind speeds and the air movement in the field is assumed to have been the same as that used in the water loss experiments. It is well known, however, that wind speed drops sharply near the ground, due to the friction and turbulance associated with the ground surface and vegetation. Furthermore, G. godeffroyi was normally partly in the burrow during the day and would be protected from much of the air movement. The assumption made is probably realistic but would produce a conservative estimate of water loss.

The second problem arose from the thermoregulatory habits of the spiders which resulted in a large temperature differential between the air and the spiders for much of the day (Humphreys, 1974). In the water loss experiments, the spiders were within 0.5° C of the ambient air temperature and the assumption could be made that the evaporating power of the air was related to the ambient saturation deficit. This is not the case when the temperature of the spider differs markedly from the air temperature. It is reasonable to assume that the evaporation drive under any conditions is the difference between the saturation vapour pressure at the temperature of the evaporating surface and the ambient vapour pressure (Schmid, 1972). With this assumption, a theoretical model was developed and is considered in Fig. 7 for a relative humidity of 30%. The positive exponential curve represents the ambient saturation deficit (mb) over a temperature range from 0° C to 50° C. The series of curves represents the evaporation drive (mb) from a surface at a series of temperatures from 0° C to 40° C, in 10° C steps, when the ambient temperature varies from 0° C to 50° C at a relative humidity of 30%. This figure shows the magnitude of the effect that temperature differentials may have on the evaporation drive. If the evaporating surface is at 40° C and the ambient air at 10° C, with a relative humidity of 30%, the evaporation drive is increased by 70.09/8.59=8.16 times. Conditions similar to these were experienced by G. godeffroyi in the winter (Humphreys, 1973, 1974).
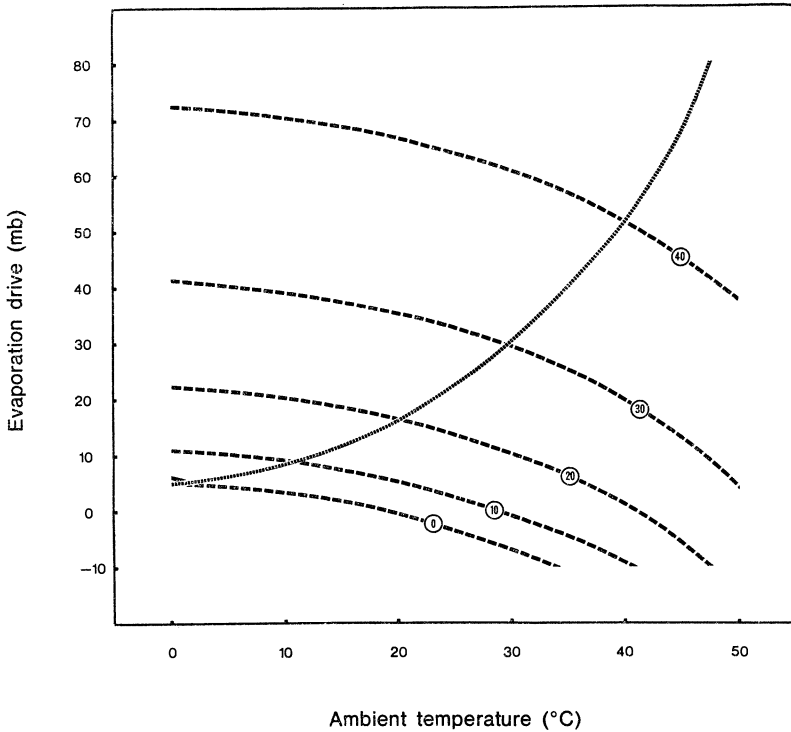
Fig. 7. Theoretical model relating the evaporation drive to temperature at 30% relative humidity when the temperature of the evaporating surface differs from the ambient temperature. The positive exponential curve represents the ambient saturation deficit (mb) between 0° C and 50° C. The series of curves represent the evaporation drive from a surface at 0° C to 40° C (with 10° C intervals) when the ambient temperature varies continuously between 0° C and 50° C. The evaporation drive is defined as the difference between the saturation vapour pressure at the temperature of the evaporating surface and the ambient vapour pressure

Experimental support for this model is provided from an experiment in which spiders were permitted access to radiant heat and their weight loss determined over 8 hrs (Table 6). On the assumption that the spiders thermoregulated at their normal temperature (34° C) the actual water loss was close to the loss predicted from the model in which the ambient temperature and the temperature of the evaporating surface differ. This model is used to derive the effective saturation deficit when adding the environmental data to the water loss model.

Environmental data were added to the regression model (Table 4) for hourly intervals and water loss estimated for each size class of *G. godeffroyi* on the 26 days, spaced throughout 1972, for which spider temperatures were available (Humphreys, 1973). No internal temperatures were available for spiders less than size class 8 and their inclusion assumes that they follow the same thermoregulatory regime as the larger spiders.

The estimated water loss over the year is expressed in Fig. 8 as the % weight loss per day for selected size classes. Taking 15% water loss as the critical level,
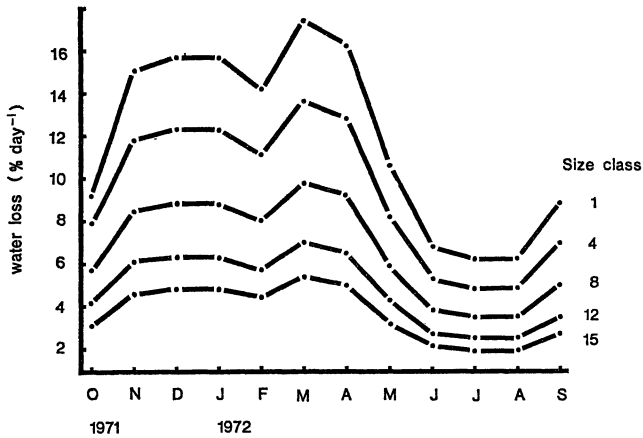
Fig. 8. Estimated water loss from *G. godeffroyi* in the field over one year. Water loss is presented as percentages of the initial body weight lost per day. Size class 1=2.5 mg and size class 15=1543 mg (Humphreys, in press)

Table 6. Comparison of actual and predicted water loss from *G. godeffroyi* when allowed to thermoregulate

Spider weight (mg)	Weight loss (mg hr^{-1})			Observed/B
	A	B	Observed	
397	0.94	1.75	1.64	0.94
507	1.16	2.16	2.31	1.07
457	1.11	2.26	2.28	1.01
272	0.71	1.45	1.77	1.22
480	1.15	2.30	1.68	0.73
507	0.96	2.17	1.87	0.86
532	0.72	2.52	2.59	1.03
396	1.03	2.01	1.17	0.58
Sum	7.78	16.62	15.31	0.92

  A) Weight loss predicted from the ambient temperature and saturation deficit.
  B) Weight loss predicted from an assumed spider temperature of 34° C and the associated evaporation drixe (see Fig. 7).

then a size class 1 spider could survive without water intake in the field for from 0.96 to 2.4 days and a size class 15 spider from 2.8 to 6.0 days, depending on the season and assuming no production of metabolic water. Altering the critical level for water results in an equivalent change in the survival time. These values are realistic because in the laboratory spiders maintained at 20° C and 60 to 70% relative humidity frequently died, the smaller spiders if not watered twice weekly and the larger ones if kept without water for a week. At 60% relative humidity and 20° C the model predicts that the spiders would lose 15% of their body weight in 2.3 and 5.6 days, respectively.

The estimated survival times appear unduly restrictive to the life of the spiders, so that it is of interest to compare the results with the estimates obtained by Shorthouse (1971) for the scorpion *Urodacus yaschenkoi*. We have seen that the rate of transpirational water loss from *G. godeffroyi* and *U. yaschenkoi* were very similar under a given set of conditions and that the behavioural strategy adopted by the two species was in marked contrast. I will assume 15% water loss to be critical in the scorpion to make the estimates comparable with those for *G. godeffroyi*; Shorthouse assumed 30% as the critical level but with no discussion. A second instar scorpion weighing 0.25 g was estimated to survive without water intake for from 3 to 10 days and a sixth instar, weighing 3.36 g, for from 7.5 to 50 days depending on the season. A size class 11 *G. godeffroyi* weighing 240 mg would survive from 3.3 to 7.8 days which is remarkably similar to the estimates for the second instar scorpion.

G. godeffroyi could survive without food in the laboratory for long periods, the larger ones for 1 to 2 months. However, Miyashita (1969a) showed that the survival time in *Lycosa T-insignita* varied with the season. The potential advantage offered by this resistance to starvation would be offset if the spiders had to rely on their food to obtain sufficient water and it is worth considering from where the spiders may obtain their water. An examination of the soil water profiles (Fig. 3) shows that the water was unavailable, that is below 11%, for long periods at any one depth. Water would have been available to the spiders at different times at different levels but was most stable at the deeper levels. The water content fell below 11% for 0.49, 0.48 and 0.41 of the time covered by the records at depths of 3, 12 and 19 cm, respectively. However, closer examination shows that water was available somewhere in the soil profile for 0.73 of the time. The burrows potentially permitted the spiders access to soil water for 24% and 44% more time than if they lived at constant depths of 19 cm and 3 cm respectively. The smaller spiders lost proportionately more water than in the larger spiders and, due to their shallower burrows had access to less of the soil water profile. Consequently they were probably more vulnerable to water loss induced mortality than the larger spiders.

Examination of the long term synoptic records for the Canberra region show that less than 2 mm of rain may fall in any month from December to May. Such low rainfall would result in soil water being unavailable to the spiders. Although the spiders potentially had access to water for longer periods through their burrowing activities, soil water alone was insufficient to maintain the spiders through a period of drought at Kowan.

The longest period during which water was not available from somewhere within the soil water profile was for 40 days in September and October 1972. None of the spiders would survive this without access to water and it is pertinent to consider the availability of water from other sources. From April to September dew forms at the Fairbairn Meteorological Station is sufficient quantities to be recorded as precipitation. It was so recorded on an average of 2.8 and 3.7 nights per month in 1971 and 1972, respectively. Dew was recorded on the Kowan field site during these months on most nights when I was present in the field. While this dew formation mainly occurs when water loss is at a seasonal low, in 1972 it coincided with a period of low levels of soil water. Dew persisted

on the field site until mid-morning in winter and was still present after the spiders had become active. Spiders readily drink free water. Dew may be important to both plants and animals in desert regions (Stone, 1963) but its potential importance in other situations has not been examined.

Consideration of Fig. 7 shows that a burrow living animal has the potential to gain water in other ways. If the animal moves from the surface at night when the ambient temperature is lower than the deep burrow temperature, due to the thermal lag in the soil, and the burrow air is saturated, then it will have a negative evaporation drive and water should condense on the surface of the animal. Experimental evidence for this was provided by Lasiewski and Bartholomew (1969). To illustrate the point I will calculate from the data of Shorthouse (1971) for the scorpion *Urodacus yaschenkoi* because they appeared to have a simple activity pattern and deep burrows so that the effect under consideration is enhanced. The scorpion lived in deep burrows in which the air was normally saturated. A scorpion returning to the bottom of the burrow in the morning could be up to 10° C colder than the deep burrow temperature. Theoretically, all the heat could be gained by the condensation of water. An adult scorpion of 3 g, with a specific heat assumed to be the same as water at 4.19 J g^{-1}, would have to gain $10 \times 3 \times 4.19 = 125.7$ J to come to equilibrium with the deep burrow temperature. The latent heat of vaporisation of water is 2260.9 J g^{-1} so that if all the heat was gained through water condensation then $125.7/2260.9 = 55.6$ mg of water would condense. From a simulation model a scorpion of this weight was estimated to lose 33 mg of water a day in summer and 5 mg in winter (Shorthouse, 1971).

Calculating from the data of Lasiewski and Bartholomew (1969) in the same manner, then the efficiency of converting this potential gain of water into actual condensate varied from 26.8% in a 5.3 g gecko (*Coleonyx variegatus*) to 47.1% in a 34.4 g spade-foot toad, *Scaphiopus couchii*. The conversion efficiency was inversely related to the weight of the animal as would be expected from the surface area to volume relationship. On this basis the conversion efficiency of a 3 g scorpion would probably be less than 25% or a gain of less than 13.9 mg of water. The effect could be increased if the scorpion moved down the burrow on several occasions, so that it potentially had the mechanism with which to survive without, as suggested by Shorthouse (1971), relying on their food supply for water. There is no evidence that the scorpions behaved in this manner or that they could utilise the condensate. Some arthropods can absorb water directly through the cuticle (Beaument, 1961) and condensing water concentrates on wettable surfaces (Burrage, 1969) so that in arthropods condensate would be differentially available on parts of the body through which it could be most readily absorbed.

The use of heat differentials for the conservation of water has been demonstrated in other ectotherms (Murrish and Schmidt-Nielsen, 1970) but only in association with anatomical adaptations. *G. godeffroyi* was sometimes found in its burrow with water condensate on the cuticle and in the laboratory it would readily clear water from the cuticle and apparently inbibe it. The water condensate may not have been produced by the mechanism discussed above, for another mechanism is available. The gaseous and liquid phases of water in the

soil only come to equilibrium at constant temperature but in soil profiles the temperature normally changes continuously. As the soil air, and often the air in deep burrows, is usually nearly saturated with water vapour (Rapoport and Tschapek, 1967), a decrease in temperature will cause droplet formation. This condensate may form on soil particles or on the spiders, in either case it may be available to them. The role of temperature differentials in the lives of ecto-therms and their potential role in the water economy of burrow living animals, both ectothermic and endothermic, would warrant investigation.

The other potential method of achieving water economy is behavioural. By remaining at the ambient temperature, instead of thermoregulating, *G. godeffroyi* should save 53.8% to 66.9% of its water loss in March and 54.6% to 66.1% in November, the saving being greater in the smaller spiders. In terms of water loss, the cost of thermoregulating is thus about 50% to 70% of the total water lost. Were water limiting to *G. godeffroyi* they would be expected to have a different behavioural strategy. Shorthouse (1971) was able to show on a simula-tion model that a desert living scorpion had an activity regime close to the ideal in terms of water loss. Whether the activity regime resulted from the con-straints of water balance is an open question.

In desert mammals nocturnalism has been considered as a method of water conservation but the work of Schmid (1972) indicates that it may not function in this way. Because the temperature differential between endotherms and their environment is greatest at night, the evaporation drive will be greatest at this time. He supported his arguments by showing that nocturnally active small mammals had urine of greater osmolarity and a relatively larger kidney medulla than diurnally active ones. It has been shown that water loss in *G. godeffroyi* should be considerably increased due to its habit of thermoregulating. Applying Schmid's arguments, thermoregulating ectotherms would be expected to show greater resistance to water loss than their non-thermoregulating neighbours but there are no comparative data available.

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Dr. W. F. Humphreys
Department of Zoology
La Trobe University
Bundoora, Vic. 3083, Australia