ON THE DRINKING OF SOIL CAPILLARY WATER BY SPIDERS

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INTRODUCTION

It is known or suspected that small arthropods and other animals which live in or on the soil, absorb soil moisture through their skins. I am not aware that it has hitherto been realized that some animals can ***drink*** soil capillary water, even against quite considerable suctions. This paper contains an account of the facility in two species of lycosid spider, and brings to light some factors upon which it depends. The spiders used were *Tarentula barbipes* (Sundevall), one of the larger British lycosids; and *Lycosa radiata* (Latreille), which is common in the south of France.

METHODS

Tarentula barbipes. The supply of animals from nature was supplemented by those bred in the laboratory. The spiders were kept separately in glass-covered 3 in. flower-pots containing soil which was kept moist by standing the pots in a large tray of water periodically replenished. Resting on the soil in each pot was a shallow waxed dish containing dry soil on which the spider normally lived. Heat and light were provided by a 3·6 W. electric bulb whose leads ran through a hole drilled through the pot. For food, drosophila, blow-fly grubs and cockroaches would all be taken provided they were not much larger than the spider itself. Mature animals were put into larger versions of the same type of cage, where the females could make the burrows within which the egg cocoons were formed; and the young were separated shortly after hatching.

Lycosa radiata was obtained in sufficient numbers from the field and has not yet been bred in the laboratory.

In preparation for an observation on drinking, a spider was put into a desiccator at room temperature (*Tarentula barbipes*) or at 35° C. (*Lycosa radiata*). Experience showed that when a spider had lost about 10% of its normal weight it would nearly always make efforts to drink when given the opportunity. A loss of 20% was usually fatal and to avoid casualties desiccation was done slowly. In the present series of experiments a spider usually remained in the desiccator for 2 days before use. It was then placed in a small capsule of cigarette paper and weighed on a chemical or torsion balance; given access to the desired moisture conditions; and then weighed again. Defaecation between the two weighings was a very rare occurrence.

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Fig. 1 shows the apparatus used in these experiments, the moisture content of the soil being controlled by the suction* applied to it. The relation between moisture content and suction for any soil was determined as follows. The apparatus was adjusted so that the sintered glass disk was level with the water in the burette and this level was then read. A dried weighed sample of soil was spread over the sintered glass to a few millimetres' depth. The soil absorbed water, and, after readjustment, the burette level was read again and the saturated water content of

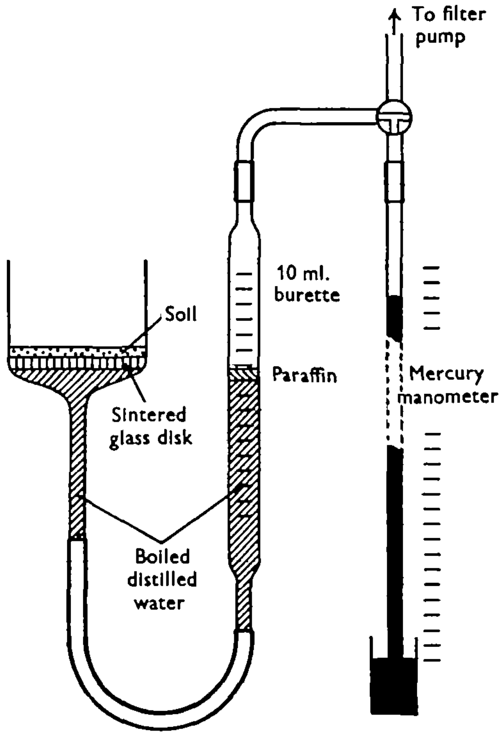

Fig. 1.

the soil thus determined. A series of burette readings was then taken at different suctions. As there was a small change of water level with suction in the absence of soil, this was determined separately and a correction made. The percentage moisture content of the soil at each suction was then found.

In most natural soils the particles, and therefore the capillaries between them, are varied in size. As the suction increases the capillaries empty in order of size, with the result that the moisture content gradually decreases. For the present purpose 'soils' of more uniform particle size were often more informative, besides giving repeatable results, and different grades of carborundum powder have been used, namely grade 100 (mean particle diameter 0·0049 in.), grade 400 (0·0010 in.)

* Throughout this paper the word 'suction' is used when referring to the reduced pressure in the soil capillaries, and is measured in mm. Hg below atmospheric pressure. Also the word 'soil' is sometimes used to cover both natural soils and carborundum powders.

and grade 600 (0·0005 in.). The moisture-suction characteristics of these powders are shown in Figs. 2–4, from which it will be seen that the moisture content remains approximately constant except over a critical range of suction, thus indicating the uniformity of capillary size.

In performing an experiment on drinking, the apparatus was first set up with the desired soil and suction. The spider, after the preliminary treatment already described, was put on the soil and if necessary watched under a binocular microscope. If the spider was left unattended, the container was covered with muslin through which there was sufficient ventilation to avoid condensation.

The standard significance tests have been used, namely the *t*-distribution and Fisher's distribution of the variance ratio.

RESULTS

Experiments demonstrating the ability to take water from soil

Table 1 shows the weight increase of desiccated adult *Tarentula barbipes* when put on to a sandy soil at various suctions and left for periods of up to a day. Significant increases occur up to a suction of 90 mm. Hg (to which the increase of 4·9 mg. relates) but not at greater suctions than this.

Table 1. *Weight increase (mg.) of* Tarentula barbipes: *uptake of water from a sandy soil*

(The spiders were all between 31 and 43 mg. in weight, and were left on the soil for varying periods up to 24 hr.)

Suction (mm. Hg)				
25–44	45–64	65–84	85–104	105–119
3·6	0·3	0·0	4·9	0·9
7·9	5·0	2·7		0·5
4·1	5·5	6·1		2·0
5·2		0·0		−1·9
		6·6		
		3·5		
		1·1		
		4·1		
		1·2		

Failure to drink from soil at high suctions may be due to two causes: there may be little water left in the soil, or the spider may be unable to overcome the suction even though plenty of water remains. These two effects are demonstrated separately with the use of carborundum powders. Figs. 2–4 show the weight increases of individual desiccated spiders (*T. barbipes*) when put on to grades 100, 400 and 600 carborundum powders at different suctions. Examination of these results, in conjunction with the moisture characteristics of the powders, suggests (*a*) that failure to drink from grades 100 and 400 above about 80 and 350 mm. respectively, is due to the powders having passed their critical points so that very little moisture is available; and (*b*) that failure to drink from grade 600 above about 450 mm., which is below the critical point of the powder, is due to the spider being unable to overcome the high suction. Evidence will be given below to show that this is not a sudden failure, but that there is a decrease in the rate of drinking with increase of suction.

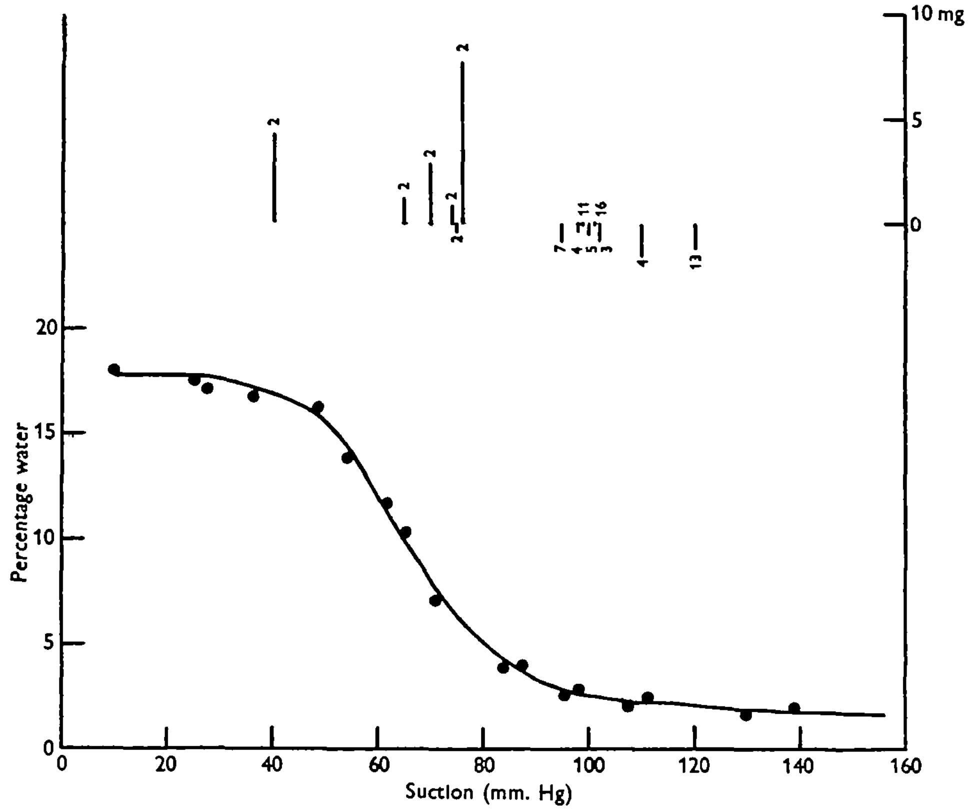

Fig. 2. The moisture-suction characteristic of grade 100 carborundum powder; and the weight increases of individual spiders (*T. barbipes*) after having been left on this powder at different suctions for the stated times (in hours).

Experiments dealing with the rate of drinking

The spiders take up a characteristic attitude while drinking, so enabling the rate of drinking to be determined. The results obtained are summarized in Tables 2–6, to which reference will be made below.

Tables 2*a* and *b* show the uptake of water during two consecutive periods of 20 min. (*T. barbipes*) or 10 min. (*Lycosa radiata*). In neither species is there a significant difference between the uptake during the initial and final periods, suggesting that such factors as fatigue and degree of desiccation do not have an important influence on the rate of drinking over the periods of time considered.

Table 3 (*Tarentula barbipes*) shows no significant difference between the rates of drinking of spiders B and D on grade 400, 150 mm. Hg; or between spiders A and B

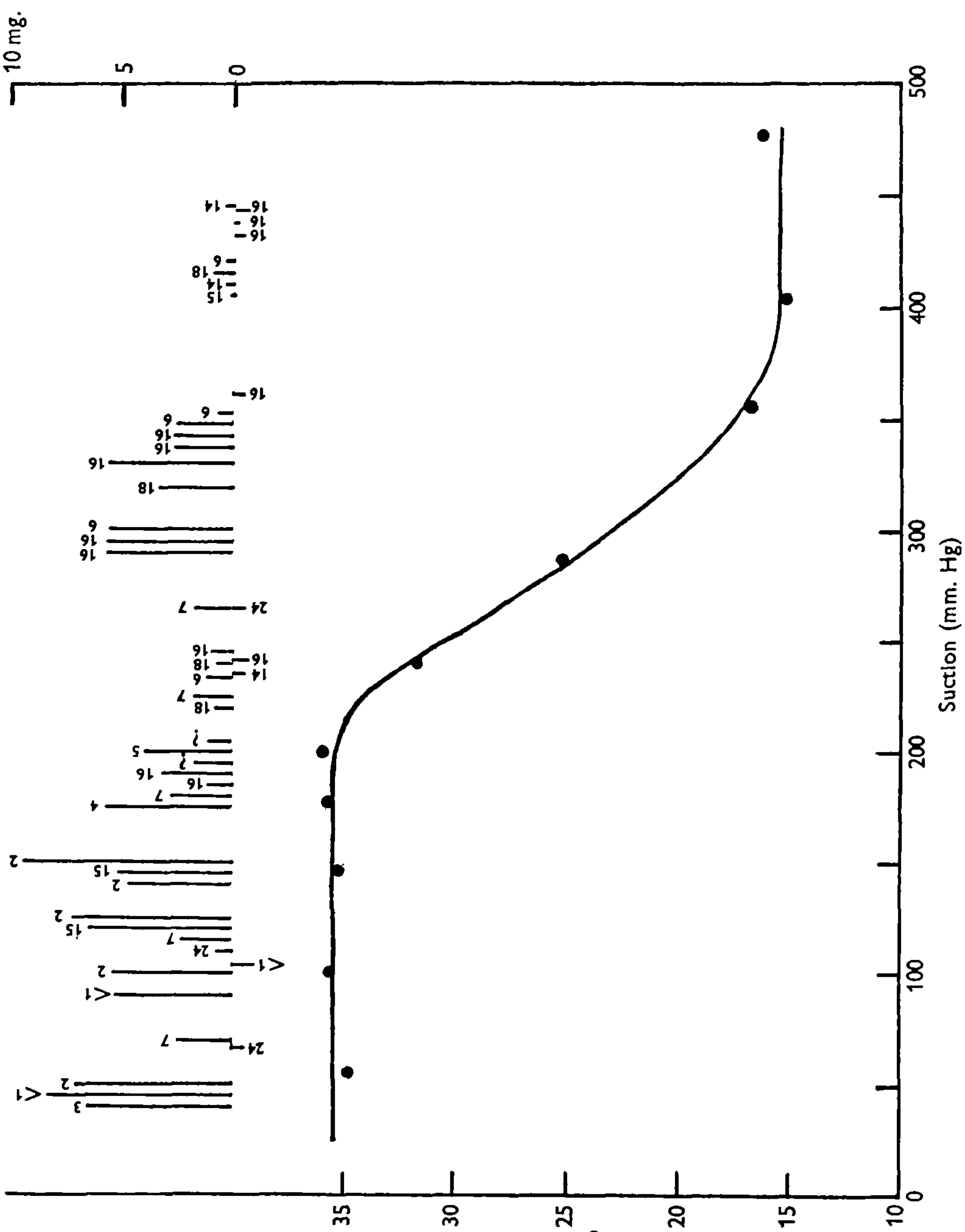

Fig. 3. The moisture-suction characteristic of grade 400 carborundum powder; and the weight increases of individual spiders (*T. barbipes*) after having been left on this powder at different suctions for the stated times (in hours).

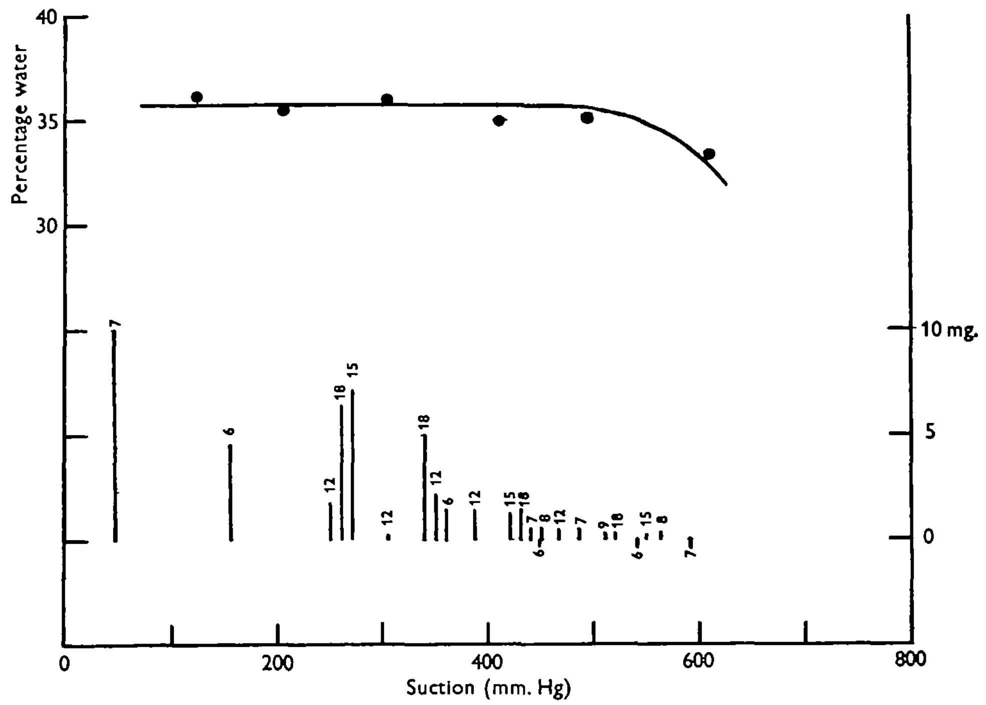

Fig. 4. The moisture-suction characteristic of grade 600 carborundum powder, and the weight increases of individual spiders (*T. barbipes*) after having been left on this powder at different suctions for the stated times (in hours).

Table 2*a*. Tarentula barbipes: *uptake of water by individual spiders during consecutive periods of* 20 *min.*

Grade	400	600	600	600
Suction (mm. Hg) ...	150	150	150	200
1st 20 min. (mg.)	2·5	3·0	2·5	1·5
2nd 20 min. (mg.)	3·0	4·0	5·0	1·5

Table 2*b*. Lycosa radiata: *uptake of water by individual spiders from* 600 *grade carborundum,* 150 *mm. Hg suction, during consecutive periods of* 10 *min.*

1st 10 min. (mg.)	14·5	17·7	8·2	12·6*	13·5	16·5
2nd 10 min. (mg.)	15·7	12·0	9·2	6·1*	11·0	12·5

* Two periods of 7 min. each.

on grade 600, 150 mm. Hg. This indicates the unimportance of unanalysed internal factors. It should, however, be noted that these spiders are of approximately the same size. Some evidence will be given below that the rate of drinking may be affected by size.

The difference in the rate of drinking of *T. barbipes* A, B and D (taken together)

Table 3. Tarentula barbipes: *rate of drinking from different grades of carborundum and at different suctions*

(m = weight increase in mg.; t = time of drinking in min. and sec.; v = rate of drinking in µg./sec.)

Suction	Grade 400									Grade 600								
	Spider A*			Spider B*			Spider D*			Spider A*			Spider B*			Spider D*		
	m	t	v	m	t	v	m	t	v	m	t	v	m	t	v	m	t	v
150 mm. Hg	2·5	17^{48}	2·3	6	28^{0}	3·6	3	30^{0}	1·7	5	16^{0}	5·2	9	30^{0}	5·0	8·5	33^{21}	4·2
				3	19^{3}	2·6	4·5	30^{0}	2·5	6	20^{0}	5·0	7	52^{0}	2·2	4·5	20^{0}	3·8
				3	40^{25}	1·2	8	20^{0}	6·7	4·5	20^{0}	3·8	3	17^{13}	2·9	1·5	12^{24}	2·0
				3	53^{3}	1·0	2·5	20^{0}	2·1	2·5	20^{0}	2·1	3	20^{0}	2·5			
				5	9^{28}	8·8	3	20^{0}	2·5	5	20^{0}	4·2	4	20^{0}	3·3			
				3·5	20^{0}	2·9	1·5	20^{0}	1·3	4·5	20^{0}	3·8	2	14^{18}	2·3			
										3	20^{0}	2·5	3	20^{0}	2·5			
Mean rates†			2·3			2·3			2·7			3·7			3·0			3·7
	2·5									3·4								
200 mm. Hg										4	20^{0}	3·3	2·5	20^{0}	2·1	3	20^{0}	2·5
													1·5	20^{0}	1·3	2	20^{0}	1·7
													1·5	20^{0}	1·3			
Mean rates†												3·3			1·5			2·1
										2·0								

* The sizes of these spiders, expressed as carapace widths, were: A = 3·5 mm., B = 3·0 mm., D = 3·3 mm.

† The mean rates shown in this and subsequent tables have been calculated from the sums of the weight increases and times of drinking, and not from the individual rates of increase.

Table 4. Lycosa radiata: *rate of drinking from different grades of carborundum and at different suctions*

(m = weight increase in mg.; t = time of drinking in min. and sec.; v = rate of drinking in μg./sec.)

Suction	Grade	Spider A*			Spider C*			Spider D*			Spider E*			Spider F*			Spider G*			Mean rates†
		m	t	v	m	t	v	m	t	v	m	t	v	m	t	v	m	t	v	
75 mm. Hg	400	15·4	20^{0}	12·8	15·4	17^{0}	15·0	21·6	16^{10}	22·3	4·8	9^{30}	8·4	11·0 6·9	11^{30} 10^{31}	16·0 11·0				14·8
	600	27·3	20^{0}	22·8	20·0 24·9	20^{0} 20^{0}	16·7 20·8	23·6 22·6	20^{0} 20^{0}	19·7 18·9	8·9	14^{58}	9·9	18·7	17^{50}	17·5	27·3	19^{45}	23·0	18·9
Mean rates†				17·8			17·6			20·1			9·3			15·3			23·0	17·4
150 mm. Hg	400	5·7	20^{0}	4·8	3·2	20^{0}	2·7	3·3	20^{0}	2·8	3·0	20^{0}	2·5	5·9 4·2	20^{0} 20^{0}	4·9 3·5				3·5
	600	2·7	20^{0}	2·3	4·5	20^{0}	3·8	1·6	20^{0}	1·3	3·5	20^{0}	2·9	6·7	20^{0}	5·6	2·5	20^{0}	2·1	3·0
Mean rates †				3·5			3·2			2·0			2·7			4·7			2·1	3·3

* The sizes of these spiders, expressed as carapace widths, were: A = 5·5 mm.; C = 5·1 mm.; D = 5·6 mm.; E = 3·7 mm.; F = 5·0 mm.; G = 5·6 mm.
† See note † at the foot of Table 3.

on grade 400, 150 mm. Hg, is not significantly different from the rates of these spiders on grade 600 at the same suction (Table 3). Similarly, there is no significant difference between the rates of drinking of the individuals of *Lycosa radiata* on 400-grade and 600-grade at either 75 mm. or 150 mm. (Table 4).

No *L. radiata* ever drank at a suction of 200 mm. Hg or over (seven observations). At 150 mm. they drank at one-fifth the rate at 75 mm. (Table 4); while the rate of drinking from a free water surface or saturated filter-paper (Table 6) was over 10 times the rate at 75 mm. Similarly, the rate of drinking of *Tarentula barbipes* from free water (Table 5) was about 10 times the rate at 150 mm.; and the small number of observations (Table 3) made at 200 mm. (which is well below the limiting suction for this species—see Fig. 4) show the rates to be significantly less than at 150 mm.

The rates of drinking of free water by both *T. barbipes* and *Lycosa radiata* (Tables 5 and 6) are significantly correlated with size. The spiders used for the

Table 5. Tarentula barbipes: *rate of drinking from a free surface by spiders of different size*

Carapace width (mm.)	Rate (μg./sec.)					Means*
4·0	37·3	58·2	50·0	53·3	—	49·7
3·5	50·7	48·3	39·3	50·1	45·8	46·8
2·8	37·5	30·8	25·0	44·4	30·7	33·7
2·5	22·0	17·1	—	—	—	} 21·4
2·5	25·0	—	—	—	—	

* See note † at the foot of Table 3.

suction experiments were not sufficiently varied in size for this effect, if present, to show itself (although *L. radiata* 'E' of Table 4 is smaller than the rest, and its rate of drinking at 75 mm., but not at 150 mm., is lower than the others).

DISCUSSION AND CONCLUSIONS

It has been shown that certain lycosid spiders can drink the moisture in soil and carborundum powders, the rate of drinking depending on the suction to which the capillary water is subject. With increasing suction, drinking becomes impossible from any particular powder, either when most of the capillaries empty, or when the suction exceeds a certain value, whichever happens first. The limiting suction, beyond which drinking is impossible even from a saturated powder, depends on the species of spider and perhaps also on the size of the individual. These results are not incompatible with the idea that for the extraction of soil capillary water a spider is dependent upon the power of its pumping stomach. This aspect of the subject will be dealt with elsewhere when the structure of the foregut is considered.

No information has yet been obtained concerning the importance of soil moisture in the natural life of spiders, and no doubt it varies with species, environment and season. For instance at the time of year when the specimens of *L. radiata* were collected for this work, the soil of the stream-bed in which they were mostly found was dry and powdery; but earlier in the summer there must have been a period after the disappearance of the running water when the soil remained moist, and this moisture may then have been used. In general, no one who has watched a desiccated spider immediately start drinking when put into moist soil, or excitedly explore the surface when the suction is too high, is likely to believe that the animal had never so acted before in its individual or racial history.

Table 6. Lycosa radiata: *rates of drinking from a free surface, grouped according to size of spider (carapace width in mm.). The horizontal lines across the columns separate the results from different spiders*

Size group ...	3·5–4·4	4·5–5·4	5·5–6·4	6·5–7·4	7·5–8·4
Rate (μg./sec.)	107 114 128 130 80 53 83 174 138 133 111 127 105 126	344 241 198 273 215 209	207 289 216 288 197 170 201 275 268 337 244 299 334 318	329 350	562 539 209 247 470
Means*	104	232	250	336	349

* See note † at the foot of Table 3.

SUMMARY

1. A study has been made of the drinking of soil moisture by two species of lycosid spider. Carborundum powders have been used to provide a 'soil' of uniform particle size.

2. The rate of drinking falls off with increase in the suction applied to the capillary water, finally becoming negligible, even though the soil remains saturated, at a suction which varies with the species of spider and possibly with the size of the individual.

3. This limiting suction is never reached if the capillaries empty at a lower suction.

4. The rate of drinking does not fall off with time, is similar for different individuals of the same species and size, and is not affected by soil particle size at a given suction, provided this is below the critical suction for the soil.

I am grateful to Dr N. Collis-George of the School of Agriculture, Cambridge, for introducing me to the method of soil-moisture determination. The observations on *L. radiata* were made at the Laboratoire Arago, Banyuls-sur-Mer, France, which I visited with the help of a grant from the research fund of King's College, and where I received every help and kindness from Prof. G. Petit and his staff.