THE EVAPORATION OF WATER FROM SPIDERS

By M. E. DAVIES and E. B. EDNEY
From the Zoology Department, University of Birmingham

(*Received* 20 *March* 1952)

(With Two Text-figures)

INTRODUCTION

Insects are generally recognized as the most successful invertebrate animals on land, but judged by the number of individuals and species, or by the range of habitats occupied, spiders are not far behind. Efficient mechanisms for water conservation are essential for the success of small animals on land, and, in particular, loss of water by evaporation must be restricted. It is well known that in insects evaporation is limited at lower temperatures by a relatively impermeable wax layer which undergoes, at a critical temperature characteristic for each species, a change in physical structure which permits a much higher rate of evaporation above this temperature.

The only information available concerning the effect of temperature on the evaporation of water from spiders is that obtained by Palmgren (1939). Using *Dolomedes fimbriatus*, he found that evaporation rises steadily with temperature, but he did not work at sufficiently high temperatures to demonstrate the presence or absence of a critical point. The present work was therefore undertaken primarily to find whether the integument of spiders behaves in the same way as that of insects, so far as restraint of evaporation is concerned, and subsidiary problems concerned the significance in this respect of the respiratory organs—the lung-book and 'tracheae'.

MATERIAL

Much of the work was carried out on the wolf spider, *Lycosa amentata* (Clerk), which was collected from the University grounds. Other species used for comparison were *Meta segmentata* Clerk, *Zilla atrica* (Koch) and *Z. x-notata* Clerk (all belonging to the family Epeiridae) which were also collected from the University grounds; and *Tegenaria derhami* Scopoli, an Agelinid, obtained from outhouses in the Birmingham district and from Surrey.

The lycosids were kept on sand, each in a separate tube to prevent cannibalism, at a relative humidity of about 75%. They were fed on *Drosophila*, and survived indefinitely. The other species were kept in similar conditions, but they were used soon after collection and were not fed.

ANATOMY OF THE RESPIRATORY ORGANS

Before attempting to measure the rate of evaporation from the integument it was necessary to know the extent to which water evaporates from the respiratory surfaces. The only information is again due to Palmgren (1939), who found that

at 17° C. and 60% R.H. only 0·01 mg. water per hour was evaporated from the lung-books as compared with 0·78 mg. from the rest of the integument, and he considered it unnecessary to seal the lung-book spiracles when measuring evaporation from the integument. He considered the amount of water evaporated from the four unbranched tracheae to be insignificant, and they were also left unsealed.

Since the number and arrangement of the lung-books varies from one species of spider to another, it was decided to study the anatomy of these organs in the species to be used in the present work, and then, should it appear necessary, to attempt to

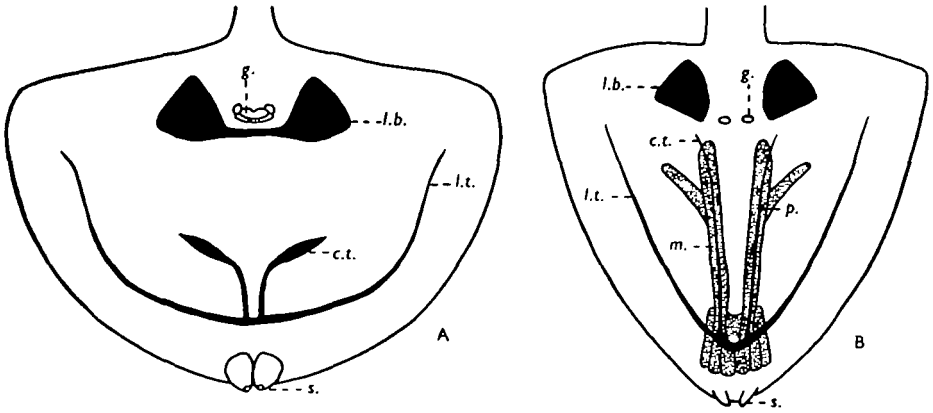

Fig. 1. Arrangement of the tracheae in (A) *Zilla atrica*, and (B) *Lycosa amentata*. Diagrammatic. *c.t.*, central trachea; *g.*, genital apparatus; *l.b.*, lung-book; *l.t.*, lateral trachea; *m.*, ventral longitudinal muscle; *p.*, attachment process; *s.*, spinerets.

measure the evaporation of water from them. In part this was a repetition of the work of Lamy (1902) and of Remy (1925) but their accounts do not contain all the information required. There is no published description of the tracheae of *Lycosa amentata*, so these will be described in some detail.

Advantage was taken of the technique developed by Wigglesworth (1950) for injecting the tracheae of insects with cobalt sulphide. This proved very successful with spiders, and permanent preparations were made of injected and bleached specimens of all the species studied. Fig. 1, which shows diagrammatically the arrangement of the tracheae in *Lycosa* and *Zilla*, is based on such preparations. (In life the tracheae follow an irregular course, moving with the contents of the abdomen.) The tracheae of *Meta* and *Tegenaria* are similar to those of *Lycosa*.

There are two pairs of unbranched tracheae in *Lycosa*, which run forwards from a vestibule, and the latter opens by a small spiracle just anterior to the spinning plate on the ventral surface. In a spider whose total length is 7·0 mm., each lateral trachea is about 2·4 mm. long, with a diameter at the base of 0·15 mm., tapering gradually to the tip, which is anchored to the body wall in the antero-lateral region of the abdomen. The terminal ninth of these tracheae is colourless after injection, and is therefore presumably solid; the rest of their length is filled with a black precipitate of cobalt sulphide, and is hollow. The central tracheae are about 1·7 mm.

long, they leave the antero-lateral corners of the vestibule and run straight forwards along the ventral longitudinal muscles. At a point about one-fifth of the total length away from the vestibule, each trachea bears a small process which serves to anchor it to the underlying muscle, and there are similar processes rather more than half-way along, providing attachment to a dorso-ventral muscle. Beyond this point the tracheae are free; they are black up to the tips in injected specimens and therefore hollow. As pointed out earlier by Remy and others, the tracheae are ectodermal invaginations, they are lined with cuticle, and their lumen is kept open by a number of small chitinous spines. The chitinous layer is surrounded by typical epidermal cells. Examination of sections cut at 10μ confirmed these observations.

The lung-books of many spiders have been adequately described (e.g. Kastner, 1924, 1929), and will not be referred to in detail here. In cobalt-sulphide injected specimens they appear intensely black, and their anatomy is best studied in fresh material with a stereoscopic microscope. Each lung-book in *L. amentata* contains from 30 to 55 triangular lamellae. An estimate of the total respiratory surface in this species was made by means of camera lucida drawings of a sample of five lamellae from each of five spiders. The mean area per spider was 9·0 mm.^{2}, though there was much variation between one spider and another owing to differences in size and in numbers of lamellae present. The highest value recorded was 12·5 and the lowest 6·7 mm^2. An estimate of the surface area of the tracheae in the same species was obtained by flattening and making camera lucida drawings as before. The mean figure was 0·30 mm^2. and the extremes were 0·33 and 0·25 mm^2. It is clear from these figures that the respiratory surface of the lung-books is approximately thirty times as great as that of the tracheae.

RESPIRATORY FUNCTION OF THE TRACHEAE

Remy (1925) used indigo blue injected in the reduced, colourless form, to demonstrate the respiratory function of the tracheae in a number of spiders. This was repeated on *Lycosa amentata*. The reduced material was injected into the abdomen and the animal was dissected under oxygen-free saline after 3 min. Both the lung-books and the tracheae were intensely blue, demonstrating the presence of free oxygen in those areas. It is clear, therefore, that oxygen does enter the body of the animal via the tracheae, and an attempt was then made to measure the amount absorbed in this way and to compare it with the amount absorbed via the lung-books.

A standard Warburg manometer apparatus was used, running at 30° C. Spiders were exposed for periods of 5 hr., one in each flask of the apparatus, and enclosed in a small muslin sac to prevent undue movement. Twelve spiders were used in each of three groups: in the first, the animals were intact; in the second, lung-book spiracles were blocked with celloidin, and in the third the openings to the tracheae were similarly blocked. Animals in the second group died after about 4 hr. Readings were made at the end of each hour, and the results were expressed as the volume of oxygen absorbed in microlitres per mg. during the whole 5-hr. period. This figure was calculated separately for each spider and a mean was then obtained.

The results (means and standard deviations) were as follows:

Intact spiders	Lung-books blocked	Tracheae blocked
2·9 (0·5)	0·0 (0·0)	3·3 (0·7)

Clearly there was a great deal of variability, and there is no significant difference between the means for intact spiders and those with the tracheae blocked. Two related facts, however, emerge—first, that there is no *measurable* uptake of oxygen through the tracheae; and secondly, that tracheal respiration, if it occurs at all, is insufficient to keep the animals alive. Now the respiratory surface offered by the tracheae has been shown above to be one-thirtieth of that of the lung-books. If the assumption is made that the permeability to oxygen of the two surfaces is similar, then one-thirtieth of 0·6 μl. of oxygen per mg. of spider will enter through the tracheae in 1 hr. A spider weighs about 20 mg., so that a total of 0·4 μl. per hour will enter the tracheae, and this amount is too small to give a significant reading on the manometer employed. The results obtained with this apparatus are not, therefore, inconsistent with those obtained by means of the indigo blue technique.

THE EFFECT OF CARBON DIOXIDE ON EVAPORATION FROM THE LUNG-BOOKS

In view of the very small tracheal surface demonstrated above it was not considered necessary to block their spiracles when measuring evaporation. The lung-books, however, present a much greater surface, and evaporation from them might be expected to form a significant proportion of the total. In insects, if the spiracles are kept open by exposing the animals to CO_2 in air, evaporation is greatly increased. It is also known that the spiracles to the lung-books in spiders are nearly closed in the resting animal and may be caused to open by exposure to CO_2 and air mixtures (Hazelhoff, 1926*a*, *b*). The following experiment was carried out to find whether such enforced opening would lead to an increased rate of evaporation from *Lycosa*.

Spiders were exposed in test tubes. Each tube was graduated into ten parts, inverted over mercury and the pressure equalized, so that mercury occupied one-tenth of the volume. CO_2 was allowed to bubble in, displacing the mercury, and each tube was then sealed with a vaselined glass slip. Several tubes were checked after preparation in this way by inverting them over KOH, when the latter rose accurately to the 10% mark. The method is simple, and critical accuracy is clearly unnecessary in an experiment of this sort.

Each tube also contained, at the bottom, a small muslin bag of calcium chloride. This was held in place by a tightly fitting gauze plate which also served as a platform for the spider. Four series of spiders, each of eight individuals, were used: in two series the animals were alive, in the others they had been killed by exposure to KCN. Both living and dead spiders were exposed either to air or to 10% CO_2 in air. Loss in weight during 24-hr. exposures was taken as a measure of the water evaporated and was expressed as a percentage of the original weight of the spider. The results (means and standard deviations) were as follows:

	Alive	Dead
In air	16% (5·2%)	19% (5·5%)
In 10% CO_2	23% (5·7%)	18% (3·8%)

There is clearly a good deal of variability, but there is a significant difference between the means for living spiders in air and in CO_2 ($p < 0.05$). There is no significant effect of CO_2 upon the rate of evaporation from dead spiders. There is a suggestion that dead spiders lose water more rapidly than living ones in air; the difference is not statistically significant, but it will be discussed further below (p. 580). The fact that living spiders in CO_2 lose more water than dead ones is explicable if the spiracles of dead spiders are not caused to open wide by CO_2.

THE EFFECT OF TEMPERATURE UPON EVAPORATION

The results obtained in the last experiment indicate that the rate of evaporation from living spiders is increased by nearly half if the spiracles are kept open. The amount of evaporation from normal (partially closed) spiracles, as compared with the rest of the integument, is still uncertain, and so is the effect of temperature upon total and spiracular evaporation. The following experiments were designed to provide this information.

(*a*) *Experiments with* Lycosa amentata

Spiders were exposed six at a time, but separated from one another, to a slowly moving stream of dry air (*ca.* 5 cm./sec.) at constant temperatures for periods of 15 min. The apparatus used was similar to that described by Edney (1951). The animals were weighed immediately before and after exposure, and the difference in weight was taken as a measure of the water lost by evaporation. None of the animals defaecated during exposure. The temperatures used ranged from 10 to 60° C. at 10° intervals. There were four groups of spiders, each consisting of twelve animals; either dead or living and either with or without the lung-books blocked.

The surface area of each spider was established by substitution in the formula $S = kW^{\frac{2}{3}}$, the constant k having been determined by camera lucida drawings of the flattened integuments of three spiders of known weight (k for *Lycosa amentata* = 12·3). Evaporation was then expressed in terms of mg./cm².hr., and the results are shown in Table 1 and Fig. 2. It should be understood that in

Table 1. *The rate of evaporation of water, in mg./cm².hr., from* Lycosa amentata *into dry air moving at* ca. 5·0 *cm./sec. Each entry is the mean of twelve determinations, followed by the standard deviation. The minimum measurable rate is approximately* 0·4, *and all means below* 0·6 *are entered as* < 0·6

Temp. ° C.	Alive		Dead	
	Lung-books blocked	Lung-books free	Lung-books blocked	Lung-books free
10	< 0·6	< 0·6	< 0·6	< 0·6
20	< 0·6	0·6 (0·1)	< 0·6	0·6 (0·4)
30	0·6 (0·4)	0·9 (0·5)	0·6 (0·3)	1·6 (0·7)
40	1·25 (0·6)	1·5 (0·5)	1·35 (0·4)	2·1 (0·8)
50	7·6 (1·0)	9·3 (2·2)	10·5 (2·8)	12·4 (1·7)
60	18·7 (3·8)	20·2 (3·0)	20·6 (2·5)	24·6 (3·0)

arriving at the figures which refer to unblocked spiders, no allowance has been made for the surface area of the lung leaflets. The extent to which these are freely evaporating surfaces is unknown, and in any case, a clearer picture of evaporation through the spiracles can be obtained if the results with and without occlusion are expressed in the same terms, i.e. per unit area of *integument*.

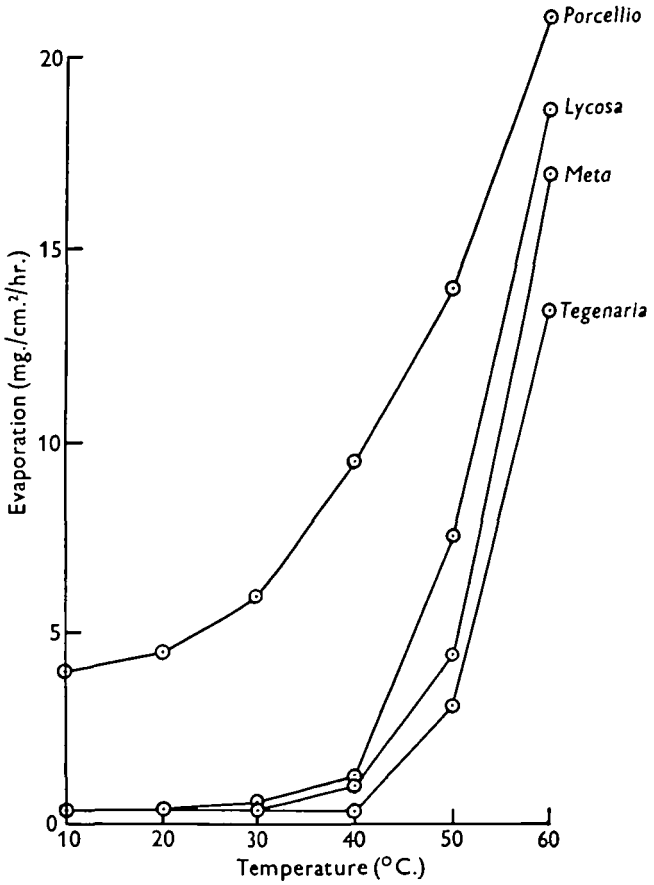

Fig. 2. The rate of evaporation from spiders exposed for 15 min. to dry air at various temperatures. Data for the woodlouse, *Porcellio*, from Edney (1951).

The weight of an individual *Lycosa* is of the order of 20 mg., and the balance used could be read to the nearest 0·1 mg. With these limits, a simple calculation shows that the lowest measurable rate of evaporation is of the order of 0·4 mg./cm^2./hr., and any value between 0·2 and 0·6 will be read as 0·4. In expressing the results, therefore, means up to 0·6 are not distinguished, but are entered as $<0{\cdot}6$ in the table, and are represented by the value 0·4 in the graph. For this reason little can be said with confidence about the results at 30° C. and below, except that the absolute amounts of water evaporated are very small. At higher temperatures, the differences between living and dead animals, or between those with the spiracles

blocked and free, are not very great; yet it is perhaps significant that wherever differences are observable they are in the same direction, and for both living and dead spiders, the rate of evaporation from intact animals is greater than that from spiders with the lung-books blocked. Furthermore, at all temperatures, the figures referring to dead spiders are higher than the corresponding figures for living ones, whether blocked or free spiders are compared.

After 15 min. exposure at 50° C. the spiders in the 'living' groups died, and they were therefore dead when exposed a few minutes later to 60° C. The fact that these spiders still show a lower rate of evaporation than the corresponding animals in the 'dead' group, which had been killed before the experiment with KCN, is discussed below (p. 580).

The most significant feature of these results from the present point of view is that whereas temperature has little effect upon the rate of evaporation up to 40° C., above this, evaporation increases rapidly, and the shape of the whole curve resembles that obtained with insects.

Six fresh spiders were exposed at intervals of 2° C. from 40 to 50° C., and the evaporation rates shown below in mg./cm.²/hr., indicate a critical temperature at the bottom of this range, since the beginning of the steep rise is already evident at 42° C.:

Temp. °C. ...	40	42	44	46	48	50
Mean	1·3	4·7	5·4	6·5	7·7	10·6
Standard deviation	0·3	1·0	1·2	0·3	0·8	0·8

The spiders used for obtaining this information differed from those to which Table 1 relates in not having been exposed at 10, 20 and 30° C. before exposure at 40° C. The absolute values obtained are not therefore strictly comparable with those shown in that Table, but the position of the break is nevertheless sufficiently clear.

(*b*) *Comparative measurements of the effect of temperature on evaporation from other species*

Comparative measurements of evaporation from the integuments of a number of different species of spider were made in the following conditions: the lung-book spiracles were blocked, the same specimens were used at all temperatures, they were exposed for 15 min. at each temperature, and only female spiders were used (since the males of some species are much smaller and usually rare). The results again expressed as mg./cm².hr., are shown in Table 2 and graphed in Fig. 2 together with the comparable figures for *Lycosa* obtained previously.

Although some of the species used in these measurements are larger than *Lycosa*, so that the minimum measurable rate of evaporation is somewhat lower, it is not considered advisable to attach significance to differences between readings lower than 0·6 mg./cm².hr., and these are again inserted in Table 2 as $<0{\cdot}6$. In Fig. 2, the value of 0·4 is again used to represent such results graphically.

For purposes of comparison, Fig. 2 also contains a curve showing evaporation from the woodlouse *Porcellio scaber* (data from Edney, 1951), and it is clear that the

curves for all species of spider resemble one another and differ from the *Porcellio* curve in showing the characteristic break at a critical temperature below which evaporation is severely restricted.

Table 2. *The rate of evaporation of water, in mg./cm².hr., into dry air moving at* ca. 5·0 *cm./sec., from spiders exposed for* 15 *min. Each entry is a mean followed by the standard deviation. The minimum measurable rate is approximately* 0·4, *and all means below* 0·6 *are entered as* <0·6

	Lycosa amentata	*Tegenaria derhami*	*Meta segmentata*	*Zilla atrica**	*Zilla x-notata**
No. of spiders used ...	12	14	12	6	6
Temp. ° C.					
10	<0·6	<0·6	<0·6	<0·6	<0·6
20	<0·6	<0·6	<0·6	<0·6	<0·6
30	0·6 (0·4)	<0·6	<0·6	<0·6	<0·6
40	1·25 (0·6)	<0·6	1·0 (0·6)	4·1 (1·2)	1·4 (0·4)
50	7·6 (1·6)	3·2 (1·4)	4·4 (0·7)	13·9 (3·3)	3·0 (0·7)
55	—	—	—	18·9 (6·6)	6·4 (1·6)
60	18·7 (3·8)	13·4 (3·3)	16·9 (2·4)	—	—

* In these two species fresh spiders were used at each temperature (see text).

Evaporation was also measured from *Zilla atrica* and *Z. x-notata*, but since these spiders did not survive repeated exposures so well as other species, fresh spiders were used at each temperature, and the results are therefore not strictly comparable with the rest, for a fresh spider exposed at a high temperature may be expected to lose more water than one which has previously been exposed to a number of lower temperatures. The method does not, of course, affect the determination of critical temperatures. The results for these two species are also given in Table 2.

THE EFFECT OF ABRASION UPON EVAPORATION

In view of the similarity in shape between these curves and those obtained with insects, the presence of a wax layer in the cuticle of spiders may be suspected. In *Rhodnius*, abrasion of the cuticle with an inert dust such as Neosyl apparently removes the wax layer and permits greatly increased evaporation. A similar experiment was carried out with *Lycosa*. Spiders allowed to move in the presence of Neosyl, dusted on them and on the floor of the container in which they were kept, were dead after 24 hr., but they survived well up to 12 hr. After 12 hr. treatment, then, the spiracles were blocked, and evaporation was measured from the integument. Six spiders were used at each of the three temperatures, 20, 30 and 40° C. The results expressed as mg./cm².hr., together with comparable figures for normal spiders, were as follows (means and standard deviations):

	20° C.	30° C.	40° C.
After exposure to Neosyl	2·3 (0·5)	3·6 (1·0)	7·0 (1·7)
Normal spiders	<0·6	0·6 (0·4)	1·25 (0·6)

The increase in rate of evaporation at each temperature after exposure to Neosyl is approximately sixfold, and leaves no doubt that a water-proofing layer has been damaged.

DISCUSSION

Information is now available about the effect of temperature and humidity upon evaporation through the integument of most important groups of terrestrial arthropods. As a result of the work of Ramsay (1935), Wigglesworth (1945) and Beament (1945) the cuticle of many insects has been shown to possess a discrete layer of wax-like material, at or near the surface (or possibly permeating the epicuticle in some species (Kramer & Wigglesworth, 1950)) which limits permeability to water at low temperatures, but which undergoes a physical change, involving loss of orientation of the surface molecules, at a critical temperature, above which evaporation is very much greater.

In the ticks, Lees (1947) has shown that essentially the same mechanism is at work. In both insects and ticks the possession of a higher critical temperature usually means a lesser permeability at temperatures in the biological range, and it is possible roughly to correlate the critical temperature with the kind of biological niche inhabited; the Argasidea, for instance, show critical temperatures which are higher than those in the Ixodidae, and members of the former family inhabit drier, warmer situations than the latter.

As regards the myriapods, Edney (1949) has shown that in the diplopod *Glomeris* there is no sharp break in the temperature-evaporation curve, and that evaporation is approximately proportional to saturation deficit. Cloudesley-Thompson (1950) obtained similar results with another diplopod, *Paradesmus*, and the conclusion is drawn that these animals do not possess a discrete wax layer, but owe to phenolic tanning the modicum of impermeability which is shown by the integument.

Amongst the Crustacea, few of which are terrestrial, the woodlice show the same properties as the diplopods so far as evaporation from the integument is concerned (Edney, 1951), and their cuticle is also believed to be without a discrete wax layer. Different species of woodlice differ as regards permeability and this may perhaps be accounted for by different degrees of tanning (though such a process has not been demonstrated).

Friedel (1928) has investigated the humidity relations of the chilopod *Scutigerella*, but he did not find the effect of temperature upon evaporation, and no information of this nature seeems to be available as regards any member of this group.

So far as arachnids are concerned, the present work on spiders has shown that they resemble ticks and insects in showing a critical temperature, and in showing a greater permeability if the superficial layers of the cuticle are abraded. There seems little doubt, therefore, that they too have a discrete wax layer, and that this has contributed to their success in occupying the drier terrestrial habitats.

It has been shown experimentally that the critical temperature for *Lycosa* is approximately 40° C. Examination of the curves for *Tegenaria* and *Meta* suggest that their critical temperatures are higher. *Tegenaria* certainly shows less than the minimum measurable rate of evaporation at 40° C., and at all higher temperatures

both species show lower rates of evaporation than *Lycosa*. In *Zilla atrica* evaporation has already begun to rise steeply at 40° C.: the critical temperature must be lower than in any other species studied, and the figures suggest 34–36° C. *Zilla x-notata* shows a less well defined critical temperature than most: it is certainly higher than that of *Z. atrica*, but at higher temperatures the rate of evaporation is lower than that of any other species studied.

Such differences as have emerged may well be correlated with habitat, but it is difficult to make such correlation with any confidence, for little is known about the climatic conditions in habitats occupied by spiders. Of the three species other than the *Zillas*, *Tegenaria* shows the highest critical temperature, *Meta* comes next, and *Lycosa* shows the lowest. If the assumption is made that a higher critical temperature denotes a lower rate of evaporation within the biological range (as it does with insects and ticks), then as regards the spiders studied in the present work, it can at least be said that there is some correlation between habitat and resistance to desiccation, for *Tegenaria* is a domestic species, living in sheds, cellars, attics and the like—habitats which often appear to be rather dry. *Lycosa* on the other hand lives in holes in the ground, and is therefore probably in a moister environment. *Meta* occupies a variety of habitats, and shows an intermediate critical temperature.

Of the two *Zillas* investigated, *atrica* shows a lower critical temperature and higher evaporation rate than *x-notata*, and *atrica* occurs on bushes and hedgerows while *x-notata* is found in buildings in the corners of windows and doorways. It seems likely that temperatures will rise higher, and humidities fall lower, in buildings than on hedgerows, but no precise information is available.

As regards evaporation from the respiratory surfaces, the present results show that, like insects, spiders may lose considerable quantities of water in this way. The spiracles leading to the lung-books are provided with closing mechanisms, but if these are kept open artificially by CO_2 (and presumably in nature as the result of activity) evaporation increases by nearly 50% of the normal figure. This is not, in fact, such a large increase as that shown by insects in similar experiments, where evaporation may be more than doubled (Mellanby, 1934).

There is, however, one respect in which spiders appear to behave differently from insects: evaporation is slightly more rapid from dead than from living animals. This effect is observed whether the spiracles are blocked or normally open (see p. 574, and Table 1). In insects, provided the spiracles are sealed, there is no difference in the rate of evaporation from living and dead animals. It seems possible that the explanation may lie in a secretory activity of the epidermal cells. Lees (1947) has shown that unfed ticks absorb water through the cuticle when exposed to relative humidities higher than 90% or so, and that the rate of loss at lower humidities than this is much less rapid if the animals are alive than if they are dead. If spiders possess a similar mechanism, then smaller loss from living specimens would be accounted for by the restraining effect of the secretory activity of the cells concerned. No direct evidence that this is the correct explanation was obtained in the present work, but if the further assumption is made that this secretory activity does not cease immediately upon

death (in the sense of loss of response to mechanical stimuli) but continues for a few minutes at least, then an explanation is available for the observation recorded in Table 1 that at 60° C., although all spiders were dead when exposed, those which had been recently alive continued to lose water less rapidly than those which had been killed by KCN before the beginning of the series of exposures.

SUMMARY

1. The purpose of the present work was to investigate and compare the water-retaining properties of the integument in a number of species of spider. Subsidiary investigations concerned the anatomy and function of the 'tracheae' as respiratory organs, and the significance of these organs and of the lung-books in total water loss.

2. The anatomy of the tracheae was investigated by means of the cobalt-sulphide injection technique. In *Lycosa amentata* they consist of four unbranched tubes, and their surface area is approximately one-thirtieth of that of the lung-book leaflets. Injection of reduced indigo blue demonstrates that O_2 enters via these tracheae, but the amount is too small to be measured by a standard Warburg manometer, and is insufficient to keep the animal alive if the lung-books are blocked. At 30° C. intact spiders absorb approximately 0·6 μl./mg./hr.

3. If the lung-book spiracles are kept open by exposing living spiders to 10% CO_2 in air, evaporation increases by nearly 50% (from 16 to 23% of body weight in 24 hr.). There is no significant increase if dead spiders are exposed, possibly because the spiracles do not open.

4. The rate of evaporation into dry air moving at *ca.* 5·0 cm./sec. was measured from dead and living *Lycosa* with the spiracles either blocked or free. The spiders were exposed for 15 min. at 10° C. intervals from 10 to 60° C. Up to 30° C. the rates in mg./cm^2./hr. were low, never more than 1·6 (dead spiders with free spiracles) and usually $< 0{\cdot}6$. The rate increases rapidly above 40° C., and at higher temperatures, although differences are small, evaporation is always greater from intact than from blocked spiders and greater from dead than from living spiders. Animals exposed at 2° C. intervals from 40 to 50° C. show the beginning of the steep rise at 42° C.—the critical temperature is therefore in this region.

5. Comparable measurements of evaporation from the integument only were made on the following species: *Meta segmentata*, *Tegenaria derhami*, *Zilla atrica* and *Z. x-notata*. Lung-book spiracles were blocked, only females were used, and the same individuals were exposed at each temperature except for the *Zilla* spp. As in *Lycosa*, the rate of evaporation from all these spiders increases abruptly at a critical temperature, and the shape of the curves is similar to that found in insects.

6. The species stand in the following order as regards critical temperatures (lowest to highest): *Zilla atrica*, *Lycosa*, *Meta*, *Tegenaria*. *Zilla x-notata* shows a less well-defined critical temperature, and a lower rate of evaporation than any other species at higher temperatures.

7. Abrasion with an inert dust produces an approximately sixfold increase in the rate of evaporation from *Lycosa*.

8. The above results are compared with similar measurements in other arthropods. Spiders resemble insects and ticks, and differ from isopods and myriapods, so far as the effect of temperature upon evaporation is concerned, and it is suggested that a discrete wax layer is probably present in the spider cuticle.

9. The suggestion that evaporation is resisted by active secretion of the epidermal cells (as in ticks) is put forward to account for somewhat greater rates of evaporation from dead than from living spiders in similar conditions.

Our thanks are due to Mr T. Savory and to Mr G. H. Locket, for confirming identifications, and for information concerning habitats. One of us (M.E.D.) was in receipt of a grant from the Department of Scientific and Industrial Research during the course of the work, and this is gratefully acknowledged.

REFERENCES

BEAMENT, J. W. L. (1945). The cuticular lipoids of insects. *J. Exp. Biol.* **21**, 115–31.

CLOUDESLEY-THOMPSON, J. L. (1950). The water relations and cuticle of *Paradesmus gracilis* (Diplopoda, Strongylidae). *Quart. J. Micr. Sci.* **91**, 453–64.

EDNEY, E. B. (1949). Evaporation of water from woodlice. *Nature, Lond.*, **164**, 321.

EDNEY, E. B. (1951). The evaporation of water from woodlice and the millipede, *Glomeris*. *J. Exp. Biol.* **28**, 91–115.

FRIEDEL, H. (1928). Ökologische und physiologische Untersuchungen an *Scutigerella immaculata* (Newp.). *Z. Morph. Okol. Tiere*, 10, 738–97.

HAZELHOFF, E. H. (1926*a*). On a new form of breathing regulation (regulation of diffusion) in insects and arachnids. *Proc. Acad. Sci. Amst.* **29**, 493–6.

HAZELHOFF, E. H. (1926*b*). *Regeling der Ademhaling bij Insecten en Spinnen*. Utrecht.

KASTNER, A. (1924). Die vergleichende anatomische Bedeutung der Interpulmonarfalte der Araneae. *Zool. Anz.* **58**, 97–102.

KASTNER, A. (1929). Bau und Funktion der facher Tracheen einiger Spinne. *Z. Morph. Okol. Tiere*, **13**, 463–558.

KRAMER, S. & WIGGLESWORTH, V. B. (1950). The outer layers of the cuticle in the cockroach *Periplaneta americana* and the function of the oenocytes. *Quart. J. Micr. Sci.* **91**, 63–72.

LAMY, E. (1902). Recherches anatomiques sur les trachées des araignées. *Ann. Sci. Nat. Zool.* B, **8**, 149–280.

LEES, A. D. (1947). Transpiration and the structure of the epicuticle in ticks. *J. Exp. Biol.* **23**, 379–410.

MELLANBY, K. (1934). The site of loss of water from insects. *Proc. Roy. Soc.* B, **116**, 139–49.

PALMGREN, P. (1939). Ökologische und physiologische Untersuchungen über die Spinne *Dolomedes fimbriatus* (Cl.). *Acta. zool. Fenn.* **24**, 1–42.

RAMSAY, J. A. (1935). The evaporation of water from the cockroach. *J. Exp. Biol.* **12**, 373–83.

REMY, P. (1925). *Contribution à l'étude de l'appareil respiratoire et de la respiration chez quelques invertébrés*. Nancy.

WIGGLESWORTH, V. B. (1945). Transpiration through the cuticle of insects. *J. Exp. Biol.* **21**, 97–114.

WIGGLESWORTH, V. B. (1950). A new method for injecting the tracheae and tracheoles of insects. *Quart. J. Micr. Sci.* **91**, 217–24.