

THE LONGEVITY OF FASTING ORIBATID MITES

BY

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INTRODUCTION.

This paper deals with the longevity of six species of fasting oribatid mites in different relative humidities at various constant temperatures. The mites were taken from the bark of trees, woodland moss, woodland litter and from a sphagnum bog (MADGE, 1961 *a* and *in preparation*). Because any one species was found mainly in one habitat, it was termed an "indicator species" of that habitat. An extensive literature review of the mites from different habitats confirmed this arbitrary grouping (MADGE, 1961 *a* and 1964 *b*). These habitats have widely differing microclimates, with marked diurnal and seasonal temperature and relative humidity changes (MADGE, 1961 *a* and *in prep.*)

This is the third of a series of papers on the physiology and behaviour of oribatid mites (for other published work see MADGE, 1964 *a* and *b*).

APPARATUS AND METHODS.

The apparatus is shown in Fig. 1. Atmospheric humidity was controlled with aqueous solutions of sodium hydroxide (MADGE, 1961 *b*) and dry air obtained with silica gel. The experimental chamber was a filter crucible with a sintered glass base (porosity 100 μ -120 μ) and a plain glass top. The crucible was pushed half way through a rubber bung, cemented into position, and the bung fitted into the top of a large glass jar packed with glass wool; this acted as a spray trap. The jar and crucible connected to a series of were conical flasks half filled with aqueous NaOH solution. A stream of air, at about 1,000 cc per minute, was circulated through the apparatus by a small electric pump, and escaped from the expe-

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rimental chamber through a gauze-covered outlet near its top into another conical flask. The atmospheric humidity inside the chamber reached equilibrium inside 30 minutes. The apparatus was left in a constant temperature room overnight before introducing the mites into it; the humidity solutions were renewed daily.

The mites were taken out of the experimental chamber at intervals and inspected with a binocular microscope ($\times 30$). Motionless animals were removed, put into

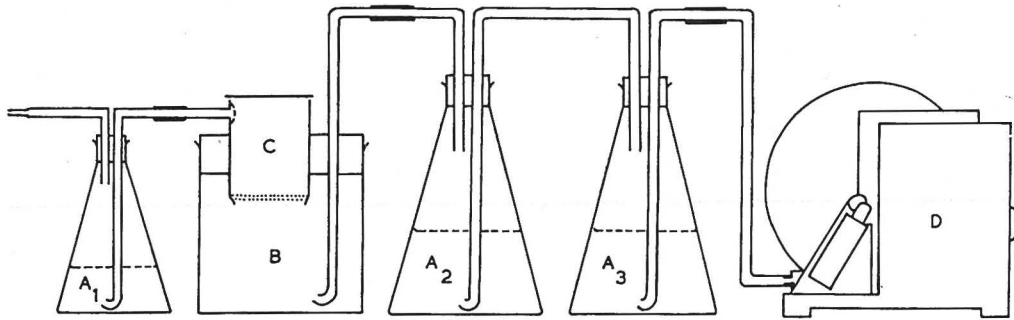


FIG. 1. — Apparatus for investigating the longevity of fasting oribatid mites in different relative humidities (saturation deficits) at constant temperatures

LEGEND A_1 - A_3 : aqueous solutions of NaOH; B: glass wool spray-trap; C: experimental chamber; D: air pump.

a culture cell and re-examined shortly afterwards. If no movements were noted they were subsequently discarded and recorded as dead. Living mites were replaced in the apparatus as quickly as possible.

The rates of water-loss in two species of mites were found by weighing them on a sensitive 5 mg torsion balance, accurate to 0.02 mg.

Stock cultures, kept at 5°C ($\pm 0.5^\circ\text{C}$) in damp plaster-of-Paris cells with debris from their natural habitat, were transferred to the experimental temperature 3-4 hours before the experiment began.

EXPERIMENTAL RESULTS.

1. Longevity in relation to temperature and saturation deficit.

General observations.

The evaporating power of the air is expressed as the "drying power" or saturation deficit of the air, which is relatively temperature-independent, rather than its "wetness" or relative humidity, which is temperature-dependent. Fig. 2 and Table 1 show the relationship between the longevity of different species of fasting oribatid mites and various saturation deficits at constant temperatures. The mean length of life was calculated from the formula $\frac{\sum (t \times n)}{\sum n}$, where t is the time of obser-

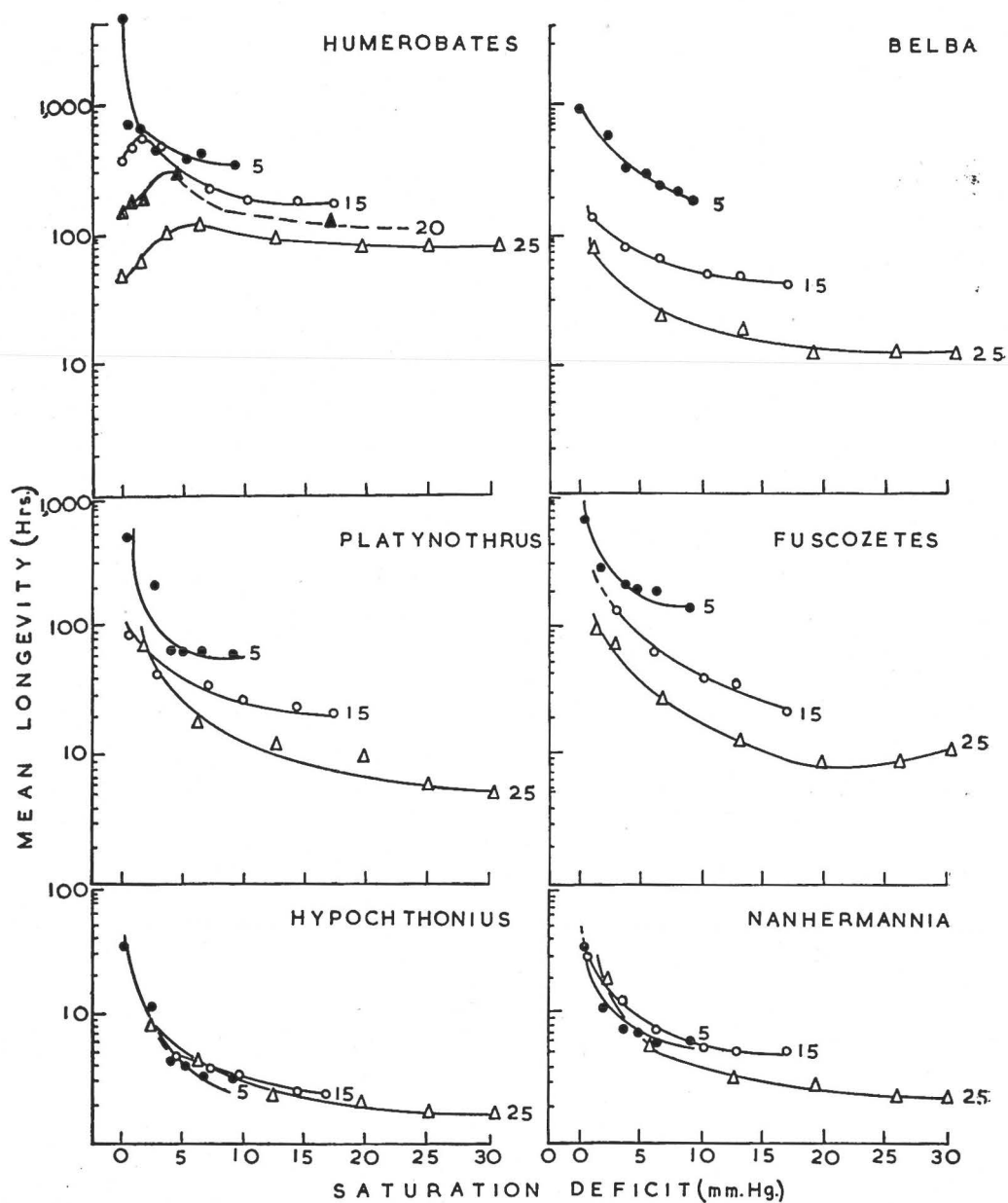


FIG. 2. — The relationship between (log) mean longevity and saturation deficit for oribatid mites at 3-4 different temperatures (the curves have been drawn by eye).

TABLE I.

The mean longevity (in hrs.) of oribatid mites in different saturation deficits at constant temperatures of 5°C (above), 15°C (middle), and 25°C (below). Number of records in brackets.

Saturation deficit (mm Hg)	8.72	6.98	5.23	3.49	1.74	0.87	0.44	0.00
Relative humidity (%)	0	20	40	60	80	90	95	100
<i>Hummerobates rostromellatus</i> G.	242.4 (7)	252.8 (9)	276.0 (9)	304.8 (9)	724.8 (14)	782.0 (14)	—	1380.0 (15)
<i>Belba geniculosa</i> Oudms.	194.4 (6)	218.4 (7)	223.2 (7)	290.4 (11)	374.4 (12)	523.2 (14)	—	>968.6 (14)
<i>Platynocheilus peltifer</i> (Koch)	64.2 (11)	67.3 (12)	67.6 (12)	73.8 (12)	121.4 (17)	—	>158.9 (18)	—
<i>Fuscozetes fuscipes</i> (Koch)	187.2 (7)	206.4 (7)	214.6 (7)	216.0 (9)	276.0 (11)	—	618.4 (9)	—
<i>Nanhermannia nana</i> (Nic.)	6.2 (12)	5.9 (12)	7.7 (13)	8.1 (13)	11.2 (14)	—	>38.0 (17)	—
<i>Hypochthonius rufulus</i> (Koch)	2.3 (12)	2.6 (13)	3.4 (13)	3.3 (14)	12.3 (23)	—	37.2 (30)	—
Saturation deficit (mm Hg)	17.06	13.65	10.04	6.82	3.41	1.70	0.85	0.00
Relative humidity (%)	0	20	40	60	80	90	95	100
<i>H. rostromellatus</i>	170.4 (12)	182.4 (14)	192.0 (14)	223.2 (18)	432.0 (18)	561.0 (7)	437.6 (7)	289.6 (14)
at 20°C	—	—	—	170.0 (12)	300.0 (20)	199.2 (18)	196.8 (18)	184.8 (18)
<i>B. geniculosa</i>	42.2 (5)	50.4 (5)	50.4 (5)	68.8 (6)	88.8 (8)	—	146.4 (12)	—
<i>P. peltifer</i>	12.3 (11)	14.9 (13)	17.7 (14)	28.5 (16)	33.9 (24)	—	>92.4 (33)	—
<i>F. fuscipes</i>	13.4 (5)	26.5 (8)	28.3 (9)	58.4 (12)	131.1 (7)	—	>52.0 (4)	—
<i>N. nana</i>	5.7 (12)	5.7 (12)	6.0 (12)	9.1 (13)	15.7 (14)	—	>31.1 (17)	—
<i>H. rufulus</i>	1.5 (8)	1.7 (8)	2.3 (10)	3.3 (12)	4.6 (16)	—	—	—
Saturation deficit (mm Hg)	31.70	25.36	19.02	12.68	6.34	3.17	1.57	0.00
Relative humidity (%)	0	20	40	60	80	90	95	100
<i>H. rostromellatus</i>	93.6 (7)	91.2 (7)	98.4 (9)	108.0 (10)	127.3 (9)	103.3 (9)	64.8 (7)	50.4 (5)
<i>B. geniculosa</i>	13.2 (5)	13.2 (5)	13.2 (5)	20.5 (6)	26.1 (6)	—	79.2 (11)	—
<i>P. peltifer</i>	5.2 (12)	5.5 (12)	10.6 (19)	12.8 (22)	16.1 (23)	—	72.8 (17)	—
<i>F. fuscipes</i>	10.1 (5)	9.1 (6)	8.3 (8)	13.6 (8)	29.7 (7)	81.2 (11)	87.8 (13)	—
<i>N. nana</i>	1.4 (5)	1.5 (5)	2.1 (10)	3.3 (13)	6.3 (8)	—	>23.0 (9)	—
<i>H. rufulus</i>	0.9 (5)	0.9 (5)	1.1 (6)	1.4 (6)	5.7 (15)	—	>7.9 (11)	—

vation in hours from the start of the experiment and n the total number of mites alive at the time of observation (calculated LD 50 values from probit transformations gave approximately the same results). The results are summarised as follows :

(1) As a rule, the lower the temperature, the longer the life. (2) At any temperature, longevity is usually greatest at low saturation deficits. However, with *Humeroabates rostromellatus* Grandjean, the mean longevity at low saturation deficits becomes shorter the higher the temperature until, at 25°C, the mean longevity in saturated air is less than half that in dry air (Table 2). (3) The mean longevity is inversely proportional to the saturation deficit, as shown by the hyperbolic-shaped curves. The correlation between saturation deficit and mean longevity breaks down at high temperatures (MADGE, 1965). Thus, when mites were exposed to the highest possible temperature for survival (i.e. their thermal death point), saturation deficit had almost no effect on longevity for either 15 minutes or 1 hour (MADGE, *loc. cit.*).

TABLE 2.

The mean longevity (in hrs.) of *H. rostromellatus* in dry air and in high relative humidities at temperatures of 5°C-25°C

Temperature °C	Relative humidity %				
	0	80	90	95	100
5	242	725	728	—	1380
15	170	432	561	438	290
20	—	300	199	197	185
25	94	127	103	65	50

Results with *Hypochthonius rufulus* (Koch) and *Nanhermannia nana* (Nic.) differed from those of the other species, in that, except for very low saturation deficits (0.44-1.6 mm Hg), the mean lengths of life in saturation deficits at different temperatures were very similar. The closeness of the curves at all temperatures suggests that temperature has little direct effect on length of life and is possibly without any effect on the rate of water-loss. Assuming that, for all the species of mites, longevity is directly proportional to water-loss, the reciprocal of longevity plotted against saturation deficit should (a) show a directly proportional or linear relationship (i.e. $\frac{\text{water-loss}}{\text{sat. def.}} = K$) and (b) pass through the origin of the axes (JOHNSON, 1942). The results, given in Fig. 3, show that for most species the lines are curvilinear and do not pass through the origin but cut the ordinate some distance above it on the 1/longevity axis. Hence, the longevity (water-loss) — saturation deficit relationship is not constant and thus water-loss is not directly proportional to saturation deficit.

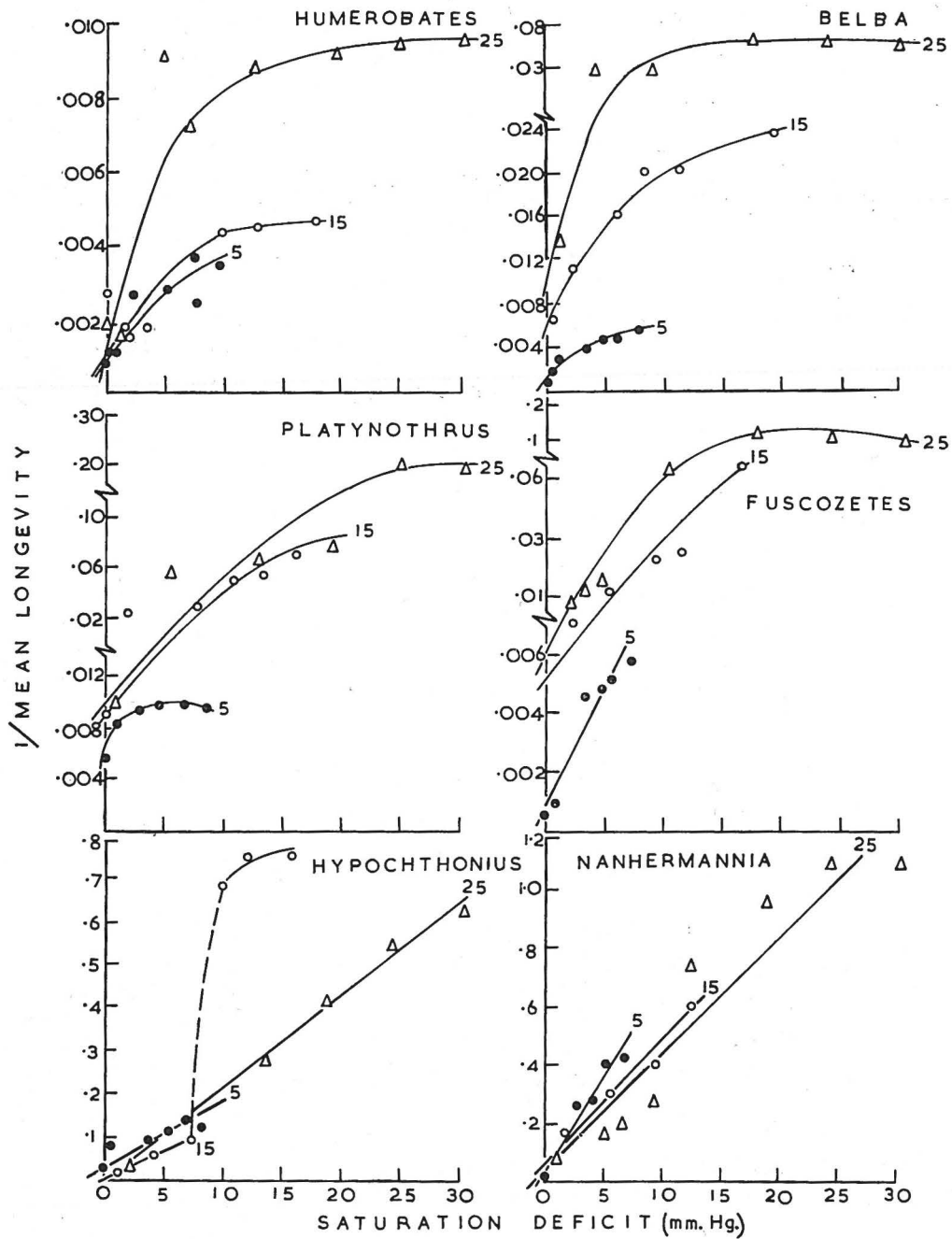


FIG. 3. — The relationship between reciprocal of mean longevity and saturation deficit for oribatid mites at 3 different temperatures.

However, the results obtained with *H. rufulus* and probably *N. nana* show that (a) it is possible to draw straight lines through the points and (b) the lines pass very near or through the origin at all temperatures. Thus, longevity appears to be directly proportional to water-loss. The results are too variable for detailed comments but nevertheless suggest that the integument of these species is permeable to watervapour while that of the remaining species is relatively impermeable.

Other experiments support these observations. It has been shown (MADGE, 1964 a) that the species other than *H. rufulus* and probably *N. nana* have an imper-

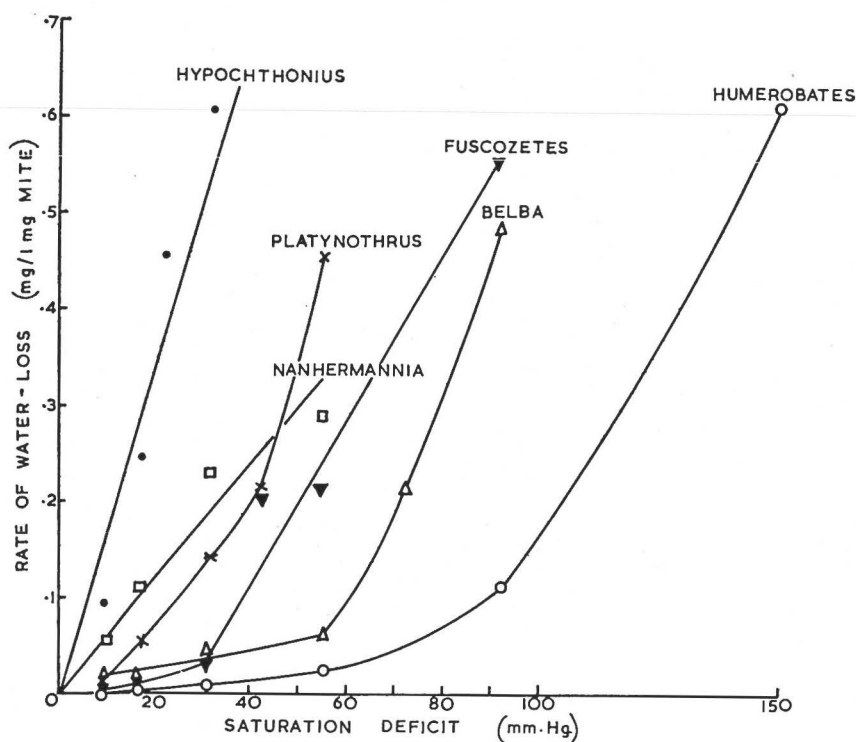


FIG. 4. — The relationship between evaporation (water-loss) and saturation deficit for oribatid mites in dry air at different temperatures (data from Madge, 1964 a).

meable wax covering over their cuticular surface. These results were obtained by plotting evaporation (as mg water-loss per 1 mg mite per 1/2 hour) against various constant temperatures from 10°C to 70°C in 0 % relative humidity; an abrupt increase in evaporation at a particular temperature (i.e. the "critical temperature") corresponded to the melting point of the waxy epicuticle. From these data, water-loss has been plotted against saturation deficit (Fig. 4). A linear relationship is apparent with *H. rufulus* and *N. nana* but with the remaining species of mites the relationship is curvilinear. Thus, the majority of the mites possess physiological mechanisms which prevent evaporation in deleterious saturation deficits, so prolon-

ging life. In *H. rufulus* and *N. nana* such mechanisms are less well-developed and hence they quickly died in any saturation deficit, regardless of temperature.

2. Longevity in relation to water-loss.

Some experiments were done with *H. rostrilamellatus* and *Belba geniculosa* Oudms. to determine the rate of water-loss by periodically weighing them for 4-7 days at constant temperatures in a range of saturation deficits. No defaecation was observed during the experiments, so loss in weight was only due to evaporation

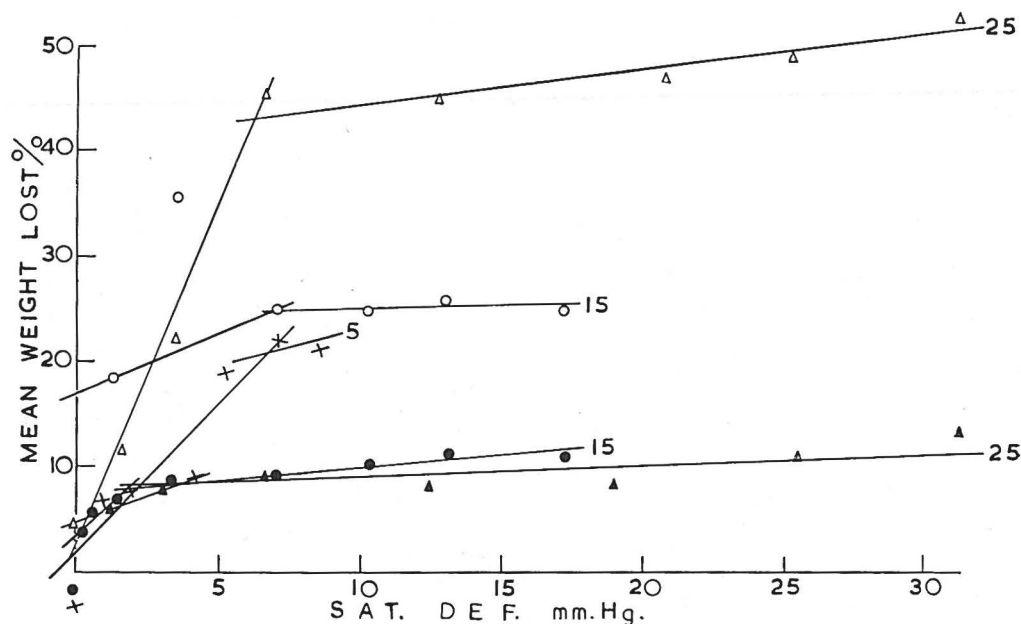


FIG. 5. — The relationship between mean weight lost (evaporation) and saturation deficit at different temperatures for *H. rostrilamellatus* and *B. geniculosa* (solid and blank symbols respectively).

of water. The results, given in Fig. 5, are summarised as follows. It has already been shown that *H. rostrilamellatus* survived 4 times longer at 15°C and 7 times longer at 25°C than did *B. geniculosa* (Table 1). During these periods, *H. rostrilamellatus* lost about half of its original bodyweight at 25°C and about a quarter at 15°C in saturation deficits of 17.1-3.4 mm Hg (0.80 % R. H.). *B. geniculosa* lost about one-tenth of its original body-weight at these temperatures in similar saturation deficits. At lower saturation deficits, *H. rostrilamellatus* lost on average about 10 % and *B. geniculosa* about 5 % of their original body-weights.

At 25°C, *H. rostrilamellatus* lost 14 times more water in dry air than in saturated air, yet survived almost twice as long in dry air (Table 2). Thus, longevity is not related to water-loss at high humidities; other factors that cause death at these

temperatures will be given later. *B. geniculosa* lost twice as much water at 5°C as at 15°C or at 25°C, yet it survived over 15 times longer at 5°C. Hence, mortality at 5°C is probably mainly caused by desiccation ; at 15°C or at 25°C it is caused by the combined effects of lethal heat and desiccation.

3. The relationship between survival-rate and natural habitat.

Table 3, taken from Table 1, shows the lethal influence of 0 % R. H. and 95 % R. H. on the mites at various temperatures. Since most of the mites were not weighed, it is not known what proportion of water the mites lost before they died, but the results nevertheless give some indication of their resistance to humidity extremes. The capacity for survival appears to be an adaptation to the general moisture conditions of their different habitats.

TABLE 3.

The mean longevity of fasting oribatid mites in dry and moist air at different temperatures

Temperature °C	0 % R. H.			95 % R. H.			Moisture availability in habitat
	5	15	25	5	15	25	
<i>H. rostromellatus</i>	242.5	170.4	93.6	598.0 ¹	437.6	64.8	Little
<i>B. geniculosa</i>	194.4	42.2	13.2	>445.4 ¹	146.4	79.2	Moderate
<i>P. peltifer</i>	64.2	12.3	5.2	>158.9	>92.4	72.8	Moderate-much
<i>F. fuscipes</i>	187.2	13.4	10.1	618.4	>52.0	87.8	Much
<i>N. nana</i>	6.2	5.7	1.4	>38.0	>31.1	>23.0	Much
<i>H. rufulus</i>	2.3	1.5	0.9	37.2	—	>7.9	Much

1. Found by intrapolation.

Thus, *H. rostromellatus*, an arboreal species living in xerophytic situations, lived 2-3 times longer in a range of dry humidities than *B. geniculosa* living in woodland litter (mesophyl), 4-18 times longer than *Platynothrus peltifer* (Koch) living in litter and sphagnum (meso-hygrophyl), and 20-80 times longer than *H. rufulus* and *N. nana* that live in a permanently wet habitat such as sphagnum (hygrophyls). High temperatures shortened life considerably with the mesophyl mites but the effect on the xerophyl species was less obvious. For instance, at 0 % R. H., *B. geniculosa* died 14 times faster at 25°C than at 5°C and *H. rostro-*

lamellatus died only 3 times faster. However, high humidities at 15°C and above were lethal to the xerophytic species (Table 2) but these humidities prolonged life considerably with the mesophyl and hygrophyl mites (Table 3). It thus seems that one of the physiological barriers preventing the distribution of *H. rostromellatus* in moist places is excessive moisture, whereas this factor favours the distribution of mesophyl and hygrophyl species. A thin-skinned hygrophyl, *H. rufulus*, was unable to cope with any humidity except the very highest since it readily lost water through a permeable integument. Hence, at any temperature it quickly died of desiccation in low humidities and of lethal heat when both temperature and humidity were high.

I have collected *Fuscozetes fuscipes* (Koch) and *P. peltifer* mainly from wet habitats but it was shown in a literature review (MADGE, 1961 *a* and 1964 *b*) that these species may also be found in a wider variety of habitats, except the very driest; they may thus equally be called meso-hygrophyl mites. Present work shows that both these species, especially *F. fuscipes*, survived much longer than "typical" hygrophyl mites such as *H. rufulus* and *N. nana*, probably owing mainly to their impermeable waxy epicuticle (MADGE, 1964 *a*).

DISCUSSION.

Early work on arthropod physiology suggested that there was a proportional relationship between death rate and saturation deficit and this led to the formulation of the "saturation deficit law" (MELLANBY, 1935). However, JOHNSON (1942) showed that the straight-line relationship need not imply proportionality, and proved that the rate of water-loss (vertical axis) in insects was a linear function of saturation deficiency (horizontal axis), the straight line obtained cutting the ordinate above the horizontal axis. The laws governing the rate of evaporation in insects are discussed in greater detail by JOHNSON (1942) and ANDREAWARTHA and BIRCH (1954).

In the majority of oribatid mites studied, the relationship between saturation deficit and longevity is hyperbolic at low temperature, tending towards linearity at high temperature. These results agree with similar experiments done with insects. However, the data obtained with three species of mites depart from the more usual kind of longevity-saturation deficit relationship. With *H. rostromellatus* a high humidity was lethal at high temperature, owing to one or a combination of the possible following factors: (1) Marked activity in moist air (MADGE, 1964 *b*), which would lead to deleterious accumulation of metabolic water in the body. (2) Another effect of continuous activity could result in food reserves being quickly utilized, leading to eventual starvation. However, this factor cannot have been the main cause of death for if food (e.g. the alga *Pleurococcus*) was provided, life was not prolonged. (3) Fungal disease: stock cultures of *H. rostromellatus* in moist plaster-of-Paris cells above 15°C were soon killed by parasitic fungi which emerged

from the mouth and anal apertures soon after death¹. Since rapid growth of entomophagous fungi only takes place in high temperature and high humidity (STEINHAUS, 1946), the mites succumbed in conditions ideal for this infection.

The results with *H. rufulus* and probably *N. nana* show that (a) at different temperatures the longevity — saturation deficit relationship is very similar, (b) the reciprocal of mean longevity and saturation deficit is linearly related and (c) evaporation in dry air at different temperatures is linearly related to the corresponding saturation deficits; the straight lines obtained in (b) and (c) passing through the origin of the axes. The evidence shows that, with these species, unlike the remaining mites, evaporation through the integument is not restricted by an epicuticular wax layer.

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SUMMARY.

1. Oribatid mites from various habitats were kept at different saturation deficits in constant temperatures of 5, 15 and 25° C.
2. The mites generally survived much longer at low temperature than at high.
3. As a rule, the lower the saturation deficit, the longer the length of life. However, at 25°C *H. rostromellatus* lived much longer in dry air than in moist air. Possible reasons for this are discussed.
4. There is a hyperbolic-shaped relationship between mean longevity and saturation deficit; the reciprocal of mean longevity and saturation deficit is curvilinear for most species and linear for *H. rufulus* and *N. nana*. Reasons for this are given.
5. The longevity of *H. rostromellatus* and *B. geniculosa* in relation to water-loss at different saturation deficits is described and discussed.
6. The mean longevity of the different species of mites in different saturation deficits is generally correlated with the amount of moisture available in their habitat.

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