

THE BEHAVIOUR OF *BELBA GENICULOSA* OUDMS.  
AND CERTAIN OTHER SPECIES OF ORIBATID MITES  
IN CONTROLLED TEMPERATURE GRADIENTS

BY

David S. MADGE.

(*Department of Zoology, University of Ibadan, Nigeria*).<sup>1</sup>

INTRODUCTION.

Many land arthropods aggregate in a specific temperature in a temperature gradient : this is their preferred temperature. This preferred temperature may become altered by desiccation, age and hunger (DEAL, 1941), aggregation (HENSON, 1960), the length of the experiment (DEAL, 1941 ; FERGUSON and LAND, 1961), and differing light intensities (KING and RILEY, 1960). It may also become changed by seasonal or diurnal variations in the temperatures of their habitats (MERKER and ADLUNG, 1958 ; E. T. and H. T. NIELSON, 1959). WELLINGTON (1949 *a* and *b*) showed that spruce budworm larvae (*Choristoneura fumiferana* Clemens) aggregated in specific evaporation zones and not in specific temperature or moisture areas. He also doubted (WELLINGTON, *loc. cit.*) the validity of the results of some previous temperature gradient experiments, on the assumption that many arthropods might have reacted mainly towards unsuspected evaporating gradients rather than to the temperature gradients that were measured.

Little work has been done on the preferred temperature of oribatid mites. PAULI (1956) found that the preferred temperature of *Belba geniculosa* was about 12° C-15° C, but other physical conditions in the apparatus were not known or controlled. WALLWORK (1960) and TARRAS-WAHLBERG (1961) also found the preferred temperature of certain species of oribatid mites.

This work is mainly an investigation of the behaviour of a common litter mite, *Belba geniculosa* Oudms. (syn. *Damaeus onustrus* Koch) in a temperature gradient apparatus. Particular attention was also paid to environmental condition other

1. Former address : Department of Entomology, Rothamsted Experimental Station, Harpenden, Hertfordshire, England.

than temperature in the apparatus. This paper is one of a series on the behaviour of oribatid mites to physical conditions (for others see MADGE, 1964 *a*, 1964 *b*, 1964 *c* and 1965).

#### APPARATUS AND METHODS.

The apparatus (Fig. 1) consisted of a copper floor, with glass sides (1 cm high), and a glass top sealed on with silicone grease. The copper runway was 22 cm long, 4 cm wide and 0.2 cm thick. Each end of the metal floor projected through and was soldered to the centre of a copper box (10 cm × 10 cm), the copper strip providing a large surface area (7.5 cm × 6.0 cm) inside the containers. The copper boxes, which had drainage outlets, fitted into two larger plywood boxes (13.5 cm × 13.5 cm) and the space in between was insulated with glass wool. Mercury thermometers fitted into the wooden lids. The copper floor was insulated outside by a thick strip of asbestos. The glass top (22.5 cm × 5.0 cm × 0.2 cm) had 10 holes 1.2 cm apart and was normally closed with rubber bungs. The lid was marked with parallel lines at 1.1 cm intervals to facilitate recordings of the distribution of the mites along the floor of the apparatus. In all the experiments the floor was lined with filter paper.

The temperature gradient was obtained by putting warm water (35° C–37° C) in one copper box and a mixture of crushed ice and salt in the other; the temperature on the floor of the experimental chamber varied within 1.5° C at the warm end and within 1° C at the cool end. The temperature along the floor and 1 mm above (latter given in brackets in text) was taken every half-hour by inserting thermistor probes through each of the 10 holes in the glass lid. The apparatus was normally kept in the dark but illuminated directly from above during readings (illuminance: 200 lux).

Groups of 50 adult and juvenile (tritonymphs) mites were usually used in experiments lasting 3 or 6 hours, each experiment being repeated several times with different batches of mites. Half-hourly records of their distribution along the temperature gradient were taken and the mites evenly distributed after each record.

Tables 1 and 2 give the evaporating gradients and relative humidities at 10 different points along the temperature gradient, i. e. 8° C–10° C to 22° C–24° C (9° C–11° C to 20° C–23.5° C) in four different experiments. Dry air was obtained with small bags of anhydrous calcium chloride and moist air with damp filter paper. The evaporation rate was measured with a modified Piche micro-evaporimeter (RUSSELL, 1906; WELLINGTON, 1949 *a*). This consisted of a water-filled capillary tube 20 cm long, bent at right angles 2 cm from one end, with a small disc of filter paper (Whatman No. 1, 4 mm diam.) adhering to its tip. The rate of evaporation of the moist filter paper disc was read off directly from a graduated millimeter scale made of stiff paper stuck on to the tube (Fig. 1). Preliminary experiments (MADGE, 1961 *a*) showed that (a) the diameter of the capillary tube was

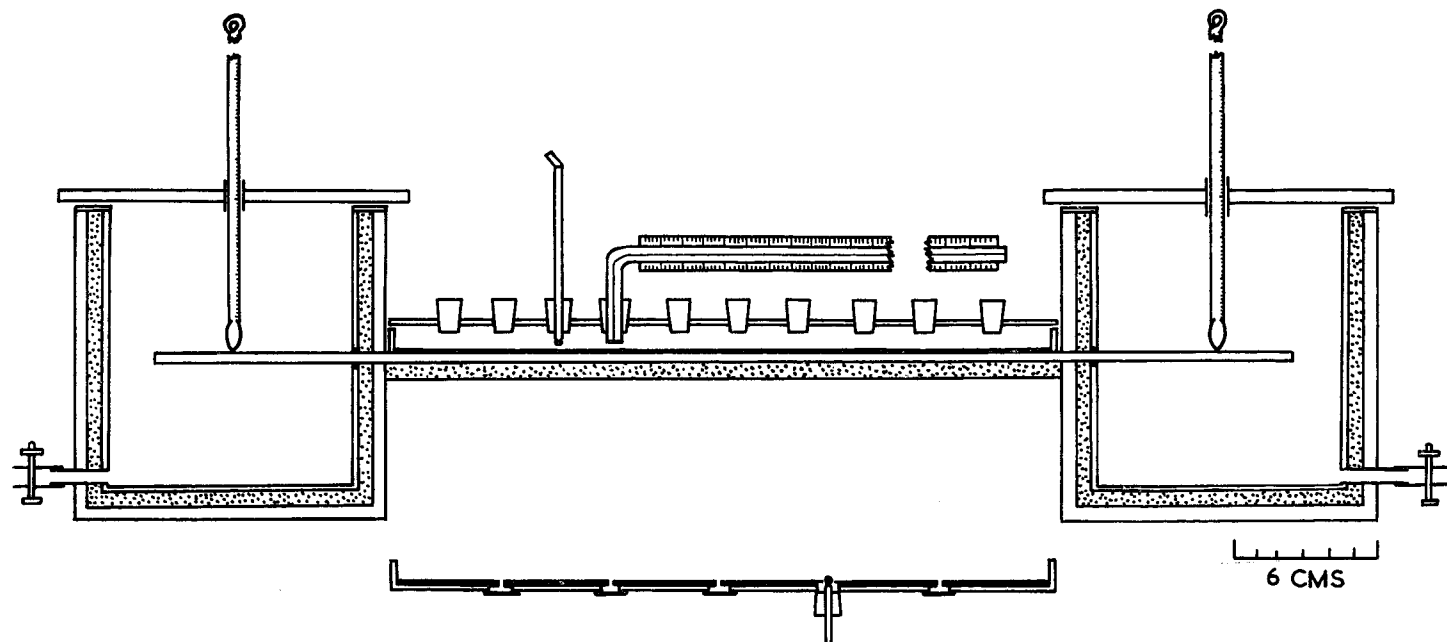


FIG. 1. — Cross-section of the temperature gradient apparatus.

constant throughout its length, (b) no water adhered to the inside of the tube and (c) by calculation, its diameter was 0.4001 mm. Attempts to find the relative humidity along the temperature gradient by calibrating the rates of evaporation of the micro-evaporimeter over known humidity solutions at different constant temperatures were unsuccessful (MADGE, *loc. cit.*), probably owing to the inte-

TABLE I.

Evaporation rates (cu mm/min) in a temperature gradient of about 9° C-23° C.

| <i>Position<br/>along<br/>gradient</i> | <i>" Saturated "</i><br><i>air</i> | <i>Dry<br/>air</i> | <i>Humidifier warm<br/>end,<br/>desiccating agent<br/>cool end</i> | <i>Desiccating agent<br/>warm end,<br/>humidifier<br/>cool end</i> |
|--|------------------------------------|--------------------|--|--|
| I<br>(warm end)                        | 0.000                              | 0.340              | 0.012  | 0.309  |
| 2                                      | 0.033                              | 0.221              | 0.038  | 0.294  |
| 3                                      | 0.040                              | 0.151              | 0.075  | 0.274  |
| 4                                      | 0.060                              | 0.138              | 0.114  | 0.239  |
| 5                                      | 0.068                              | 0.133              | 0.130  | 0.221  |
| 6                                      | 0.078                              | 0.126              | 0.141  | 0.214  |
| 7                                      | 0.088                              | 0.121              | 0.151  | 0.209  |
| 8                                      | 0.093                              | 0.116              | 0.176  | 0.198  |
| 9                                      | 0.095                              | 0.113              | 0.201  | 0.189  |
| 10<br>(cool end)                       | 0.099                              | 0.100              | 0.221  | 0.178  |

TABLE 2.

Relative humidities (%) in a temperature gradient of about 9° C-23° C.

| <i>Position<br/>along<br/>gradient</i>                     | I<br>(warm<br>end) | 2   | 3   | 4   | 5   | 6  | 7  | 8  | 9  | 10<br>(cool<br>end) |
|--|--------------------|-----|-----|-----|-----|----|----|----|----|---------------------|
| <i>" Saturated " air</i>                                   | 100                | 100 | 100 | 100 | 100 | 98 | 96 | 94 | 92 | 89                  |
| <i>Dry air</i>   | 0                  | 1   | 2   | 5   | 9   | 12 | 15 | 17 | 20 | 22                  |
| <i>Humidifier warm end,<br/>desiccating agent cool end</i> | 100                | 99  | 98  | 97  | 96  | 90 | 84 | 76 | 41 | 3                   |
| <i>Desiccating agent warm end,<br/>humidifier cool end</i> | 0                  | 16  | 40  | 49  | 60  | 69 | 80 | 87 | 89 | 100                 |

TABLE 3.

The mean distribution of adults (*above*) and nymphs (*below*) of *Belba geniculosa* Oudms. in temperature gradients of about 8° C to 22° C at various humidities in different experiments.

| Gradient<br>type                                      | Relative position in temperature gradient (2.1 cm intervals) |      |      |      |      |       |      |      |      |               | Number<br>of<br>replicates | Number<br>of<br>mites<br>per<br>replicate | Variance<br>(P) | Least significant<br>difference |       |        |
|---|--|------|------|------|------|-------|------|------|------|---------------|----------------------------|---|-----------------|---------------------------------|-------|--------|
|   | 1  | 2    | 3    | 4    | 5    | 6     | 7    | 8    | 9    | 10            |                            |   |                 | 0.05                            | 0.01  |        |
|   | (warm<br>end)  |      |      |      |      |       |      |      |      | (cool<br>end) |                            |   |                 |                                 |       |        |
| “ Saturated ” air                                     | 2.7  | 2.3  | 3.3  | 8.0  | 19.3 | 30.0  | 62.7 | 98.3 | 69.0 | 9.3           | 3 × 6                      | 50  | 39.4**          | 29.11                           | 39.19 |        |
|   | 0  | 0    | 0.5  | 11.5 | 46.5 | 98.5  | 61.5 | 32.0 | 15.0 | 5.5           | 2 × 4                      | 50  | 6.2**           | 33.41                           | 40.01 |        |
| Dry air   | 3.0  | 12.7 | 7.7  | 13.0 | 24.7 | 25.7  | 39.0 | 33.3 | 30.3 | 12.0          | 3 × 6                      | 50  | 2.4*            | 39.92                           | 44.44 |        |
|   | 1.5  | 2.5  | 5.0  | 7.0  | 33.0 | 68.0  | 86.5 | 46.5 | 9.6  | 6.5           | 2 × 4                      | 50  | 0.8             | 40.96                           | 58.26 |        |
| Humidifier warm end,<br>desiccating agent cool<br>end | 1.2  | 4.5  | 6.5  | 7.7  | 31.0 | 40.3  | 62.2 | 56.3 | 47.2 | 19.5          | 6 × 12                     | 50  | 9.3**           | 24.73                           | 33.31 |        |
|   | 6.0  | 8.3  | 15.0 | 25.3 | 54.3 | 64.0  | 53.0 | 30.8 | 40.5 | 6.8           | 4 × 8                      | 50  | 4.6**           | 46.34                           | 52.41 |        |
| Desiccating agent warm<br>end, humidifier cool<br>end | 4.5  | 7.3  | 13.0 | 21.0 | 33.5 | 48.3  | 67.8 | 45.0 | 26.5 | 14.0          | 4 × 8                      | 50  | 9.1**           | 23.01                           | 30.99 |        |
|   | 0.8  | 2.3  | 4.0  | 11.5 | 21.3 | 43.0  | 71.5 | 39.0 | 19.3 | 10.3          | 4 × 8                      | 50  | 6.3**           | 29.09                           | 39.18 |        |
| Adults adapted<br>for 48 hrs. at<br>(“saturated” air) | 0.8°C  | 9.3  | 7.0  | 17.7 | 35.0 | 47.7  | 79.7 | 50.3 | 28.3 | 22.7          | 5.3                        | 3 × 6                                     | 50              | 1.2                             | 71.05 | 96.90  |
|   | 5°C  | 4.5  | 21.5 | 24.0 | 68.5 | 100.5 | 31.0 | 23.5 | 13.0 | 8.5           | 0.5                        | 2 × 4                                     | 50              | 2.1                             | 74.25 | 104.78 |
|   | 25°C   | 9.0  | 15.5 | 18.5 | 25.0 | 42.0  | 48.0 | 55.5 | 35.0 | 17.5          | 8.0                        | 2 × 4                                     | 50              | 10.4**                          | 51.77 | 73.64  |
| Radiant heat<br>(“saturated” air)                     | 4.0  | 4.5  | 4.0  | 8.0  | 12.5 | 24.0  | 55.0 | 70.0 | 28.0 | 12.0          | 2 × 23                     | 30-40                                     | 7.4**           | 29.90                           | 42.01 |        |
|   | 3.0  | 6.0  | 4.5  | 9.5  | 13.0 | 20.5  | 39.0 | 40.0 | 48.0 | 25.5          | 2 × 23                     | 30-40                                     | 4.7**           | 25.56                           | 38.04 |        |

\* Significant at 5 %.

\*\* Significant at 1 %.

N. B. Temperature differences between each experiment varied by  $\pm 3^\circ$  C.

reaction of the different physical factors inside the apparatus. Consequently, the relative humidity was found with a small modified Edney paper hygrometer or, when possible, by calculation. Frequent checks of evaporating gradients and relative humidities were made during actual experiments; these results obtained corresponded within 5 per cent to those given in Tables 1 and 2.

## EXPERIMENTAL RESULTS.

### (1) *Preliminary Experiments.*

Initially, experiments were done at constant temperature (15° C) to show the effects of thigmotaxis by putting 50 mites at either (a) 10 equidistant points along the apparatus, or (b) all in the middle, or (c) all at one end. Some clustering was evident in all the experiments but it was least obvious in the first. Hence, in subsequent experiments the mites were evenly distributed along the whole temperature gradient.

In a temperature gradient of 15° C-30° C the mites aggregated at the cool end; in a temperature gradient of 6° C-14° C they clustered near the warm end. Thus, a temperature gradient of about 8° C-22° C ( $\pm 3^\circ$  C) was considered most suitable for the detailed experiments. Mites at either the warm end or the cool end of the latter gradient showed no effects of heat stupor or chill coma respectively.

### (2) *Detailed Results.*

Fig. 2 shows the frequency distribution of adults and nymphs of *B. geniculosa* kept in the temperature gradient apparatus for 3 hours, and also shows how other physical factors vary in such a gradient in different experiments. Table 3 gives a statistical analysis of the results of each group of experiments, which are summarised as follows:

In "saturated" air (Fig. 2, a), there was a peak frequency distribution of about 60 % at 13.5° C-15° C (14° C-15.5° C) for the adults and 12.0° C-15° C (13° C-15.5° C) for the juveniles. This region corresponded to 85 %-91 % relative humidity and an evaporating gradient of 0.07-0.10 cu mm/min. A similar distribution was maintained in other experiments lasting for six hours. It is noteworthy that in a relative humidity gradient of 10 %-95 % at a constant temperature of 15° C (MADGE, 1964 b), the adult mites invariably chose 95 % relative humidity with an evaporating gradient of 0.03 cu mm/min, whereas in a temperature gradient they chose a slightly lower temperature in apparently detrimental humidities and evaporating gradients.

In dry air (Fig. 2, b), the adults chose 11.5° C-15° C (15.5° C) and the nymphs 11° C-12° C (12° C-13° C). Here again, the mites ignored lower regions of evaporation (e. g. 0.10 cu mm/min; 0 %-5 % relative humidity at 8.5° C), selecting

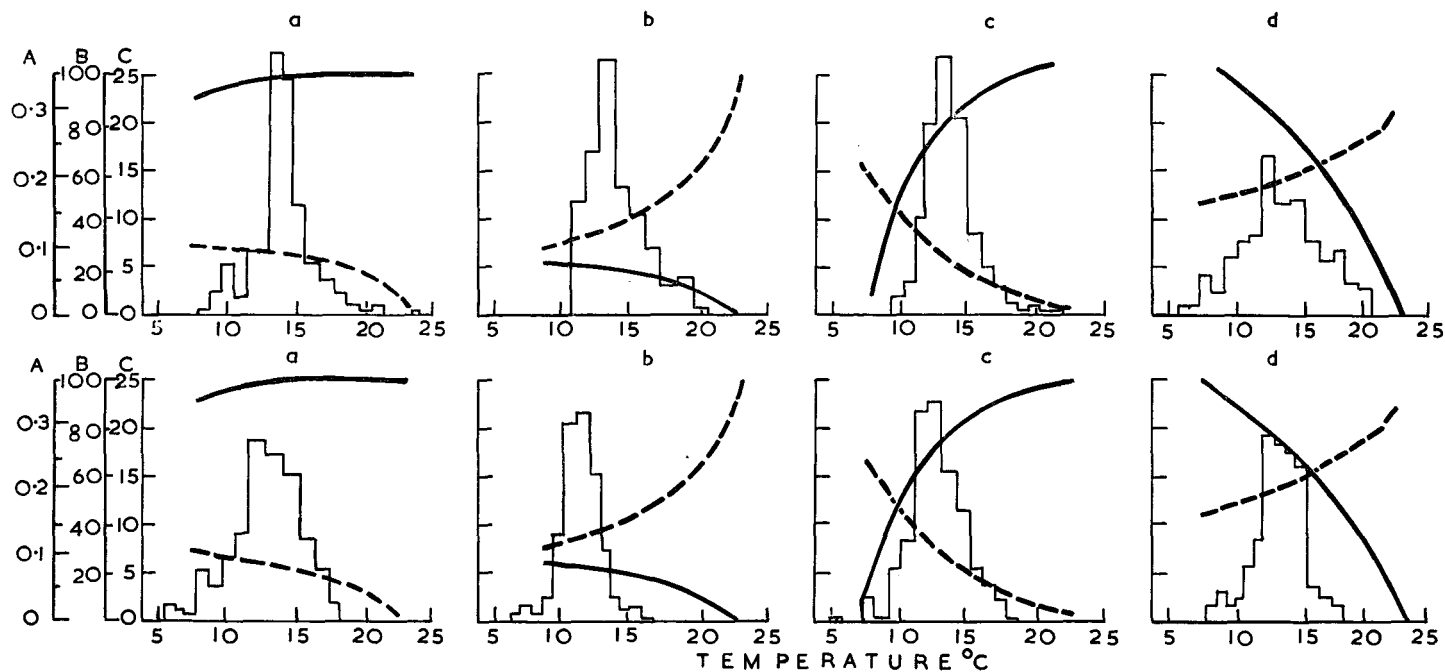


FIG. 2. — The distribution of adults (*above*) and tritonymphs (*below*) of *Belba geniculosa* Oudms. in a temperature gradient of about 8°C to 22°C under various evaporation rates and relative humidity gradients in four different sets of experiments (see Table 3). A : evaporation rate in cu mm/min (broken line) ; B : relative humidity % (solid line) ; C : frequency distribution % (histogram).

an evaporation zone of 0.12-0.13 cu mm/min and 12 %-15 % relative humidity. In these experiments, the mites remained more scattered than in "saturated" air, and the results were generally inconclusive.

In a third experiment (Fig. 2, c), when the humidifier was put in the warm end and the desiccating agent in the cool end, temperatures of 11.5° C-15° C (15.5° C) and 13° C-14° C (13.5° C-14.5° C) were chosen by the adults and juveniles respectively. The evaporating rate at these temperatures was 0.13-0.18 cu mm/min and the relative humidity 70 %-95 %. Experiments lasting for six hours gave similar results.

Finally, when the desiccating agent was put in the warm end and the humidifier in the cool end (Fig. 2, d), the adults aggregated in 11° C-15.0° C (14° C-15° C) and the nymphs in 12° C-15° C (12.5° C-15° C), which corresponded to 70 %-90 % relative humidity and an evaporating zone of about 0.21 cu mm/min. More humid air and a lower evaporating rate in lower temperature were once more ignored, suggesting that the mites again clustered in their preferred temperature, avoiding other more equable physical conditions.

#### *Preferred Temperature of Individual Mites.*

Table 4 gives the results obtained with single mites in "saturated" air, 10 readings being taken at 15 minutes intervals for each mite. Compared with groups of mites (Table 3), the preferred temperature of single adults was about 1° C higher and of single juveniles 2° C lower. Thus, thigmotaxis and/or other behaviour effects in the group experiments changed the preferred temperature of this species to a limited extent.

TABLE 4.

The distribution of individual *B. geniculosa* in a temperature gradient in "saturated" air. A total of 60 fifteen-minute readings shown.

| <i>Position along gradient</i>          | 1    | 2    | 3    | 4    | 5    | 6    | 7    | 8    | 9    | 10   |
|---|------|------|------|------|------|------|------|------|------|------|
| <i>Adults</i>                           | 0    | 0    | 0    | 1    | 1    | 4    | 7    | 8    | 6    | 3    |
| <i>Nymphs</i>                           | 0    | 0    | 0    | 1    | 1    | 2    | 3    | 7    | 10   | 6    |
| <i>Floor temperature °C</i>             | 21.4 | 20.0 | 18.9 | 17.6 | 16.3 | 15.1 | 14.0 | 13.0 | 12.0 | 10.0 |
| <i>Air temperature °C</i>               | 20.1 | 19.3 | 18.0 | 17.3 | 16.2 | 15.8 | 14.7 | 14.0 | 13.1 | 12.0 |
| <i>Relative humidity % (calculated)</i> | 100  | 100  | 100  | 100  | 100  | 98.3 | 92.4 | 89.7 | 86.3 | 83.1 |
| <i>Evaporation rate cu mm/min</i>       | 0.00 | 0.03 | 0.04 | 0.06 | 0.07 | 0.08 | 0.08 | 0.09 | 0.09 | 0.10 |



*The Effect of Desiccation and Temperature Adaptation.*

Adult mites were desiccated over phosphorus pentoxide at 15° C for 16-40 hours and then put in the temperature gradient apparatus in "saturated" air (Table 5). They aggregated mainly in 11.4° C-12.4° C (12.7° C-13.4° C), the relative humidity there being about 83 %-90 % and the evaporating gradient 0.08-0.09 cu mm/min. The results showed that there was a slight change in the preferred temperature compared with undesiccated mites (Table 3).

Other adult mites were left at constant temperatures of 0.8° C, 5° C and 25° C in moist plaster-of-Paris cells for 2-3 days with food and then put in the temperature gradient apparatus in "saturated" air. The results (Table 3) were too variable for detailed comments (results for 0.8° C and 5° C were not statistically significant), but there is no clear indication that the mites were adapted to any previous temperature.

TABLE 5.

The distribution of desiccated adult *B. geniculosa* in a temperature gradient in "saturated" air. Five different groups of 35-50 mites were used (P : 5.7\*\* ; L. S. D. (mean) 0.05 : 40.19 ; 0.01 : 54.08).

| <i>Position along gradient</i>              | 1    | 2    | 3    | 4    | 5    | 6    | 7    | 8    | 9    | 10   |
|---|------|------|------|------|------|------|------|------|------|------|
| <i>Total number of mites</i>                | 33   | 31   | 39   | 53   | 104  | 182  | 302  | 245  | 147  | 61   |
| <i>Mean number of mites</i>                 | 6.6  | 6.2  | 7.8  | 10.6 | 20.8 | 36.4 | 60.4 | 49.0 | 29.4 | 12.2 |
| <i>Percent number of mites</i>              | 2.8  | 2.6  | 3.3  | 4.3  | 8.7  | 15.3 | 25.2 | 20.4 | 12.3 | 5.1  |
| <i>Floor temperature °C</i>                 | 20.5 | 18.8 | 17.3 | 16.1 | 14.8 | 13.3 | 12.4 | 11.4 | 10.2 | 8.4  |
| <i>Air temperature °C</i>                   | 18.5 | 17.3 | 16.5 | 15.7 | 14.8 | 14.5 | 13.4 | 12.7 | 11.9 | 10.6 |
| <i>Relative humidity %<br/>(calculated)</i> | 100  | 100  | 100  | 100  | 97.4 | 96.0 | 93.7 | 90.6 | 89.0 | 85.2 |

*The Effect of Radiant Heat.*

In this experiment, the temperature gradient was arranged so that all the heat came from above. The apparatus (Fig. 1, bottom) was a shallow glass trough (20 cm × 3.5 cm) with glass sides (1 cm high) and a glass base, having 5 equally spaced holes in the floor ; these were inlets for thermistor probes but were otherwise sealed with greased coverslips. The floor of the trough was covered with moist filter paper and the trough fixed to the underside of the copper strip of the temperature gradient apparatus and sealed with silicone grease. Under these conditions, the air and floor temperatures were found to be similar. Therefore, there was no heat flow and radiation was the only important form of heat transference.

The results, given in Fig. 3 (and Table 3), showed that about 50 % of the adults aggregated in 12.5° C-13.5° C and about 50 % of the nymphs aggregated in 10.0° C-13.0° C. When the temperature range was shifted by 2° C, the peak frequency distribution shifted correspondingly (Fig. 3). Since the air was completely saturated, this aggregation was caused only by temperature. In a control experiment at 15 °C, the mites remained dispersed. The mites thus clearly reacted to radiant heat. Further comments will be given later (see general discussion (2)).

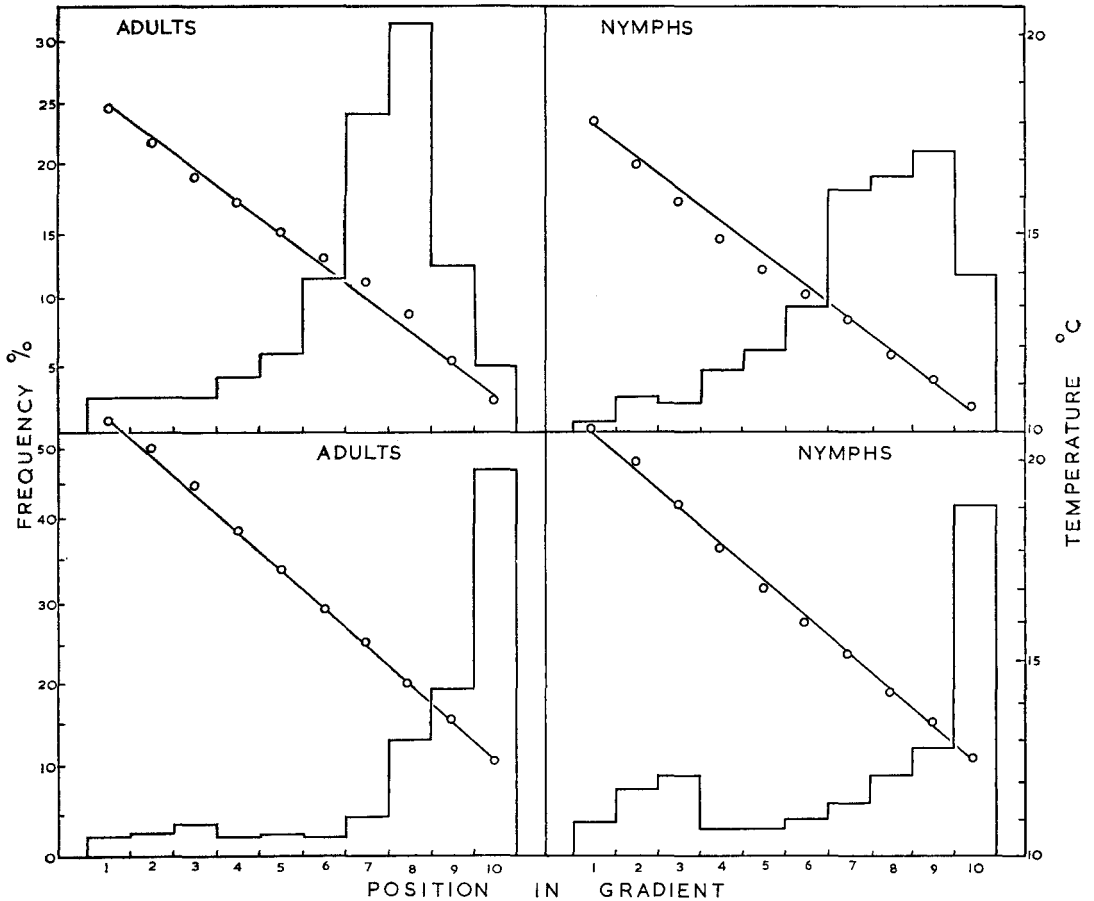


FIG. 3. — The frequency distribution of *B. geniculosa* in a gradient of radiant heat, in saturated air. Two different temperature gradients were used : (1) 10.5° C-18.5° C (above) and (2) 12.5° C-20.5° C (below).

#### *Results with Other Species of Oribatid Mites.*

Fig. 4 gives the results obtained with three other species of adult oribatid mites, namely *Humerobates rostrilamellatus* Grandjean, *Platynothrus peltifer* Koch and *Fuscozetes fuscipes* Koch in a temperature gradient of about 8° C-22° C in "satu-

rated" air. Experiments in dry air (not given) gave similar results. In either humidity, the preferred temperature of *H. rostralamellatus* was about 17° C-21° C (18° C-21° C), that of *P. peltifer* was about 10° C-14° C (12° C-13° C) and that of *F. fuscipes* was about 15.5° C-20.5° C (17° C-20° C). WALLWORK (1960) was

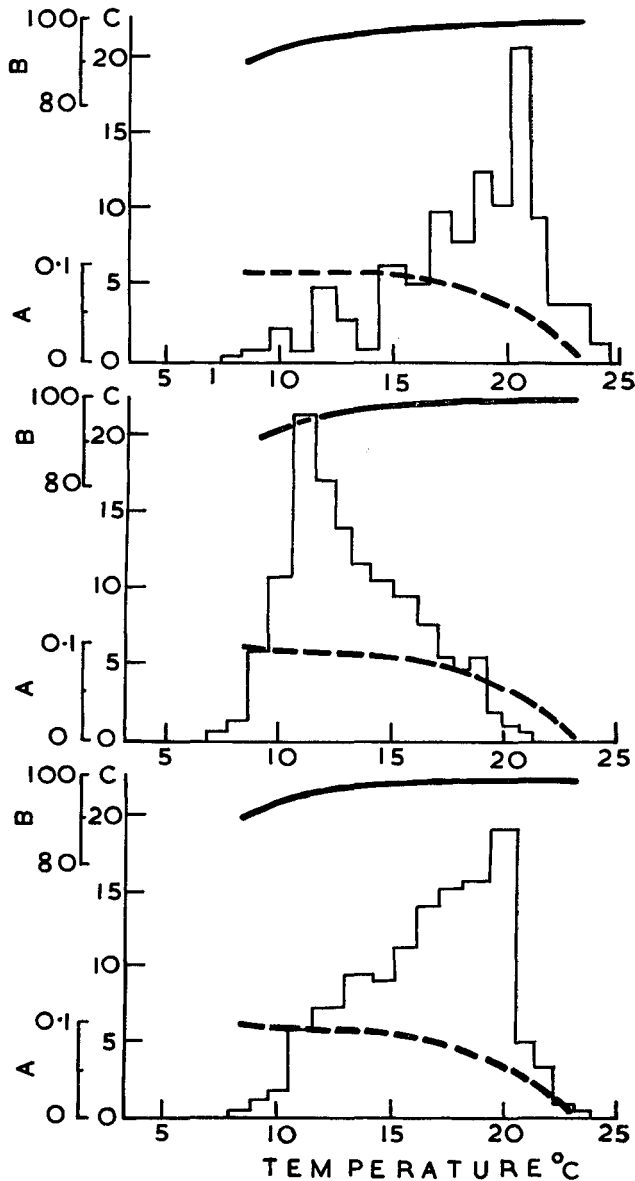


FIG. 4. — The distribution of three species of oribatid mites in a temperature gradient in "saturated" air. Legend as in Fig. 2. The mites were (above) *Humerobates rostralamellatus* Grandjean, (middle) *Platynothrus peltifer* Koch and (below) *Fuscozetes fuscipes* Koch.

unable to find a clear preferred temperature with the last named species. Thus each species had a characteristic preferred temperature that remained unchanged in either "saturated" air or dry air.

#### GENERAL DISCUSSION.

##### (1) *Theoretical Considerations and Practical Limitations in the Use of Closed Temperature Gradients.*

In the past, stable conditions have often been assumed to exist in closed temperature gradients. In fact, this is not so (MADGE, 1961 *b*). Due to the "energy flow" in such gradients, a dynamic system will be created and maintained. First, the temperature-humidity balance inside the apparatus cannot be ignored. Stable humidity will only be obtained if the atmosphere within is either completely saturated or completely dry. Otherwise, a temperature gradient will lead to an inverse humidity gradient, with dry air at the warm end and nearly saturated air at the cool end (GUNN, 1934). Arthropods may hence react to either humidity or temperature, or to both. Secondly, the difference between floor and air temperature has sometimes been ignored and arthropods, especially large ones, may react to either or both of these. To overcome this, DEAL (1941) made a "false floor" above the metal floor; the effective temperature was thus intermediate between the floor and air temperature. Thirdly, it is often assumed that a moist filter paper lining or a damp sponge inside a temperature gradient apparatus will completely saturate the atmosphere inside. However, a convection air current (or heat flow) from the warm to the cool end, accentuated by differences in air and floor temperature, creates a humidity gradient in which the relative humidity in the "cool half" of the apparatus is less than 100 %. Since the air above the floor is cooler than that of the base in the "warm half", the moisture there will evaporate and condense on to the roof of the chamber. The air in the "cool half", being warmer than that of the floor, will condense on to the floor of this region. Arthropods may thus react to the presence of free-water in the apparatus. Lastly, they may also either be attracted or repelled by the warm air-flow from the warm end to the cool end of the gradient. The various physical environmental factors thus created inside a closed temperature gradient apparatus make final analysis of the behaviour of arthropods under such conditions difficult. Hence, aggregations in any particular region cannot be attributed to temperature only, unless other physical factors are known and deliberately varied.

##### (2) *Comments on the Preferred Temperature of Belba geniculosa.*

In a temperature gradient, many terrestrial arthropods choose a preferred temperature (UVAROV, 1931; FRAENKEL and GUNN, 1940; DEAL, 1941; CARTHY, 1958, etc.). Amongst the Acarina, the British harvest mite, *Trombicula autumnalis* Shaw chose 16° C-20° C (JONES, 1950) but the sheep tick, *Ixodes ricinus* L.

aggregated only in the coldest region of the apparatus (LEES, 1948). NORGAARD (1951) found that the preferred temperature of two species of spiders, *Lycosa pul-lata* Cl. and *L. piraticus* Cl. was 28° C-36° C and 18° C-24° C respectively, and these results were related to the microclimates of their natural habitat.

However, owing to inadequate precautions being taken (see (1) above) many arthropods may also react to other physical factors whose variation depends upon temperature. Thus, WELLINGTON (1949 *a* and *b*) found that the spruce budworm, *Choristoneura fumiferana* Clemens, aggregated in regions of constant evaporation which were relatively independent of temperature and he suggested (see also ANDREWARTHA and BIRCH, 1954, p. 133) that, with few exceptions, many results attributed to temperature were obtained without the influence of humidity being known. But there is at least one well-authenticated case where temperature had an overriding influence on humidity (GUNN, 1934).

TABLE 6.

Environmental conditions at the peak frequency distribution of adults (*above*) and nymphs (*below*) of *B. geniculosa* in a temperature gradient of about 8° C-22° C. Results obtained in a relative humidity gradient at constant temperature are also included for comparison.

| Gradient type                                      | Evaporation<br>rate<br>cu mm/min | Relative<br>humidity<br>% | Temperature °C |      |
|--|----------------------------------|---------------------------|----------------|------|
|  |                                  |                           | Floor          | Air  |
| Constant temperature                               | 0.03                             | 95                        | 15.0           | 15.0 |
| “Saturated” air                                    | 0.09                             | 85-89                     | 14.3           | 14.8 |
| Dry air  | 0.12                             | 15-17                     | 13.3           | 15.5 |
| Humidifier warm end,<br>desiccating agent cool end | 0.16                             | 74-84                     | 13.3           | 15.5 |
| Desiccating agent warm end,<br>humidifier cool end | 0.20                             | 69-87                     | 13.0           | 14.5 |
| Radiation  | 0.00                             | 100                       | 13.0           | 13.0 |
| Constant temperature                               | 0.03                             | 95                        | 15.0           | 15.0 |
| “Saturated” air                                    | 0.08                             | 88-91                     | 13.5           | 14.3 |
| Dry air  | 0.12                             | 12-15                     | 11.5           | 12.5 |
| Humidifier warm end,<br>desiccating agent cool end | 0.14                             | 84-96                     | 13.5           | 14.0 |
| Desiccating agent warm end,<br>humidifier cool end | 0.21                             | 69-87                     | 13.5           | 13.8 |
| Radiation  | 0.00                             | 100                       | 11.5           | 11.5 |

TABLE 7.

Mean additive data showing the preferred temperature (range in brackets of *B. geniculosa* in a temperature gradient of about 8° C-22° C). Other physical factors at this preferred temperature are also given.

| STAGE                          | ADULTS           | NYPHHS           |
|--------------------------------|------------------|------------------|
| Floor temperature °C           | 13.5 (11-15)     | 13.0 (11-15)     |
| Air temperature °C             | 15.1 (14-15.5)   | 13.7 (12-15.5)   |
| Evaporation rate<br>cu mm/ min | 0.145            | 0.14             |
| Relative humidity %            | 65.3             | 68.9             |
| Radiant heat °C                | 13.0 (12.5-13.5) | 11.5 (10.0-13.0) |

In this work, a study has been made on the reactions of adults and nymphs of *B. geniculosa* towards various combinations of temperature, relative humidity and evaporating gradients in a small temperature gradient apparatus. The peak frequency distribution of the mites always fell within a narrow range of temperature regardless of the marked variations of other environmental factors in the apparatus (Table 6). Thus, a real temperature preference was shown which was relatively independent of other known physical factors. Table 7 gives the grand mean results for both adults and nymphs, showing that the preferred temperature of the adults was 0.5 °C higher than for the nymphs; with the experiments on radiant heat it was 1.5° C higher. The adults aggregated in a region where the relative humidity was about 4 % lower and the evaporating rate 0.005 cu mm/ min higher than that of the juveniles.

Like many arthropods, the preferred temperature of adult *B. geniculosa* was lowered by over 2° C by desiccation when compared to untreated mites. These results confirmed the susceptibility of this species to desiccation, for it has been shown elsewhere (MADGE, 1964 *b*) that as little as 6 hours desiccation had a pronounced effect on the humidity reactions of the mites. Recently TARRAS-WAHLBERG (1961) showed that the preferred temperature of the oribatid mite *Diapleurobates humeralis* (Herm.) increased in a low humidity. When the humidity was 100 % it was about 12° C-17° C but when the humidity was 30 % the preferred temperature changed to 20° C-27° C. This behaviour is unexpected, for presumably the mites lost more water at the higher temperature, but the results may have been complicated by the existing air current.

Acclimatization of *B. geniculosa* to different temperatures was ill-defined and the results in the temperature gradient were inconclusive. Other experiments (MADGE, 1965) have shown that this species is unaffected by temperature accli-

matization. WALLWORK (1960), however, found that temperature acclimatization altered the temperature reactions of certain species of oribatid mites.

Many arthropods show no responses towards radiant heat but this factor markedly affected the behaviour of *B. geniculosa*. With a very small arthropod such as an oribatid mite, the heat transfer coefficient is very large and hence, for practical purposes, the difference between the body-temperature and that of the air surrounding it is negligible (PARRY, 1951; DIGBY, 1955). Calculated data, based on DIGBY's (1955) results with a "black body" temperature showed that, for an arthropod the size of *B. geniculosa*, the difference between its (black) body-temperature and that of the air is between 0.1° C-0.01° C (Appendix I). Owing to its size, the temperature of the mite will be determined by that of the air and not directly by radiation. Thus, the behaviour of the mites towards radiant heat is similar to their reactions towards air temperature, and since there is little or no re-radiation, their surface temperature will depend mainly on air temperature. Under these conditions, the adults aggregated in 12.5° C-13.5° C and the juveniles aggregated in 10.0° C-13.0° C. The apparatus was completely saturated (there was no difference between floor and air temperature), so this was a true temperature response.

Detailed analysis of the different experiments (not given) showed that the adults responded to the combined effects of floor and air temperatures, whereas the juveniles responded mainly to the floor temperature. These results may be interpreted by comparing their behaviour under natural conditions. The body-surface of the adults is usually free from debris, but that of the juveniles is covered with debris (MADGE, 1964 *a*). Thus, the body-sensilla of the juveniles are probably non-functional while those of the adults act as thermoreceptors all over the body, including the legs. The thermoreceptors of other Acarina (e. g. *Ixodes ricinus*) are also located all over the body, including the legs.

In a temperature gradient, klinotactic orientation was shown by various Acarina. In a temperature gradient in "saturated" air, *B. geniculosa* orientated by orthokinesis and klinokinesis. Klinokinesis was noted with this species of mite in a humidity gradient at constant temperature (MADGE, 1964 *b*); it is thus not known if in the present experiments this is a humidity or temperature response, or both. Clustering behaviour, or thigmotaxis, generally had little marked effect in the temperature gradient experiments.

The behaviour of *B. geniculosa* and the other species of oribatid mites in temperature gradients is correlated with the microclimate of their habitats. This will be dealt with in a subsequent paper (MADGE, in preparation).

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## SUMMARY.

1. This paper describes the reactions of a common litter-inhabiting oribatid mite, *Belba geniculosa* Oudemans, in a small temperature gradient apparatus.
2. Notwithstanding marked differences in relative humidity and evaporating gradients inside the experimental chamber in different experiments, both the adults and the juveniles (tritonymphs) invariably aggregated in a narrow temperature range of 11.0° C-15.0° C (mean 13.5° C) and 11.0° C-15.0° C (mean 13.0° C) respectively.
3. Desiccation lowered the preferred temperature of adult mites by over 2° C when compared to normal mites.
4. Acclimatization to various temperatures had little effect on the preferred temperatures of the mites.
5. Individual mites had a slightly different preferred temperature from groups of mites.
6. Reactions to radiant heat were well-marked, the adults choosing 13° C (range 12.5° C-13.5° C) and the juveniles 1.5° C less (range 10.0° C-13.0° C).
7. A brief account of the orientating mechanism of *B. geniculosa* in the temperature gradient apparatus is given.
8. Three other species of oribatid mites chose characteristic preferred temperatures, which were similar in either dry or moist air.
9. Some theoretical considerations and practical limitations in the use of closed temperature gradients are given.
10. It is concluded that *B. geniculosa* has a true preferred temperature, irrespective of other prevailing physical environmental conditions.

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# APPENDIX I.

Assuming that an arthropod with a body temperature  $T_b$  is contained in an enclosure with a wall temperature  $T_w$ . If walls and arthropod behave as black bodies, gain of radiation per  $\text{cm}^2/\text{sec.}$  of arthropod surface is

$$\sigma (T_w^4 - T_b^4),$$

where  $\sigma$  = Stefan's constant ;  $T$  in degrees Kelvin.

If arthropod body temperature is constant, an equal amount of heat must be lost by convection to the surrounding air at temperature  $T_a$  ; i. e. if heat transfer coefficient is  $h$  (heat exchange/ $\text{cm}^2/\text{sec.}$ ), then

$$(T_w^4 - T_b^4) = h (T_b - T_a).$$

By binomial expression,

$$h (T_b - T_a) \simeq 4 \sigma T_b^3 (T_w - T_b).$$

Except in very still air, for very small arthropods  $h$  is much greater than  $4 \sigma T_b^3$ , so  $T_b - T_a$  will be much less than  $T_w - T_b$ .

Digby (1955) provided artificial radiation of  $1.5 \text{ cal./cm}^2/\text{min.}$  equivalent to radiation lost when  $T_w - T_b \simeq 150^\circ$ . For spheres with  $d < 1 \text{ mm.}$ ,  $T_b - T_a < 1^\circ \text{ C.}$

Hence, for values of  $T_w - T_b$  in Madge's experiments,  $T_b - T_a$  will be much less than  $1^\circ \text{ C.}$ , corresponding to  $0.1^\circ \text{ C.}$  to  $0.01^\circ \text{ C.}$ , since  $d$  is about  $1 \text{ mm.}$  with *Belba geniculosa* Oudms.