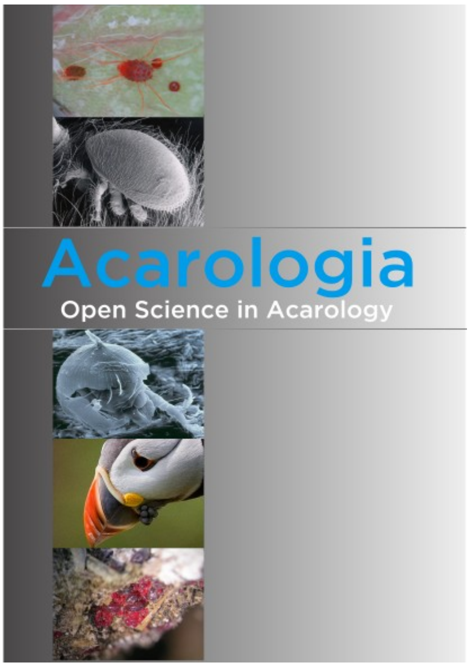

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THE SIGNIFICANCE OF THE SENSORY PHYSIOLOGY OF ORIBATID MITES IN THEIR NATURAL ENVIRONMENT

BY

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This is the last of a series of papers (for others, see MADGE 1964 *a, b, c*; and 1965 *a, b, c*) on the sensory physiology and behaviour of oribatid mites. Investigations have shown that their behaviour is far from simple and involves the interaction of several environmental factors. However, the intensity of stimulation arising from these different factors varies considerably, so that a certain behaviour pattern may be changed to another, as the result of the influence of an over-riding stimulus.

Belba geniculosa Oudms.

Fig. 1 gives some indication of the intricate behaviour of one species studied in detail, namely *Belba geniculosa* Oudms. The diagram undoubtedly oversimplifies the variability in the behaviour pattern but illustrates its complexity. For convenience, the main aspects of the reactions of this species towards controlled environmental conditions in the laboratory will be summarised before dealing with the significance of its sensory mechanisms.

In the laboratory, mites with a normal water-balance show a marked preference for a narrow temperature range irrespective of the existing, often deleterious humidity and evaporating gradients. These results are surprising since the mites move quickly to the highest humidity available in a humidity gradient at constant temperature. Individual mites behave very differently from batches of mites in similar humidities. Batches of mites quickly stop moving in their preferred high humidity owing to close contact with each others' bodies, but single mites increase in speed and continually move about in the same humidity. Activity is lower in dry air than in moist, but the number of random turns is greater. When offered a choice

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of different sand fractions in saturated air, the mites always move to the coarse sand. However, in a humidity gradient with a high humidity above fine sand and a low humidity above coarse sand, they choose fine sand in preference to coarse. When given a choice of a dry or a moist surface, the mites choose the dry one ; they nevertheless choose coarse, moist sand in preference to fine, drys and. The mites are sensitive to horizontal light but not to dorsal light, moving towards dim light and away from bright light. Finally, they react to gravity by moving downwards. Hence, certain external stimuli have an over-riding influence over others in the following order of decreasing magnitude : 1) temperature, 2) relative humidity, 3) contact and 4) moisture.

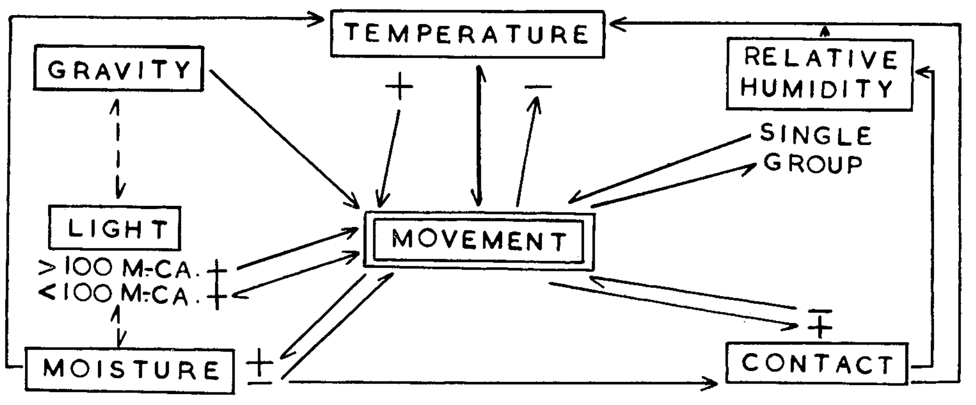

FIG. 1. — The behaviour of *Belba geniculosa* Oudms. to some environmental factors.

What follows is an attempt to evaluate the significance of the sensory physiology of *B. geniculosa* in relation to prevailing conditions in its natural habitat. This species is restricted to the humus layer of woodland litter where the humidity is high throughout the year, seldom falling below 80-90 % (Todd, 1949). The average humidity during sampling was probably higher than usual owing to the exceptionally wet weather during 1960. Furthermore, the hygroscopic properties of dead leaves provide suitable high humidities for longer than expected (VAN HEERDT, 1950). Small humidity fluctuations are quickly detected by the mites, especially differences in high humidities. This reaction undoubtedly helps to drive them away from unfavourable humidities to the deeper and therefore moister environments. Furthermore, if the mites become slightly desiccated owing to unfavourable conditions, this humidity-reaction becomes much intensified. Since mites are sensitive to air currents (TARMAN, 1959), they will tend to restrict their movements to situations where damp, still air is liable to exist.

Temperature is probably the most important environmental factor in their habitat. In the laboratory, the mites choose a narrow range of relatively low temperature (adults 13.6° C ; juveniles 13.0° C) which is slightly higher than the average annual temperature (11.5° C) of the litter layer in their habitat. Since the vertical temperature gradient from the litter to the soil surface is not large, i.e. about 3° C in summer and less than 1° C in winter, orientation is probably unaffected by small temperature fluctuations within the vegetation lattice (MADGE, *in preparation*). Other work with *B. geniculosa* has shown that they tolerate temperature extremes well above or below that of their environment. For instance, they all survived at 39° C or at -5° C for one hour in saturated air, and remained alive at 35° C for over twelve hours. The highest daily temperature recorded in the litter layer from January 1960 to April 1961 was 20.8° C (in June 1960), and it fell below freezing (-1.7° C in January 1960) on only one occasion (MADGE, *loc. cit.*).

The overriding influence of temperature gradients on humidity gradients may be explained as follows. *B. geniculosa* lives in litter that may become dry on the surface, but which retains a high moisture-content only a short distance below. The litter-temperature gradient is much less steep than the humidity gradient for the same depth. Hence, although humidity and temperature are both important to the mites, reactions to temperature gradients and humidity boundaries are more useful to them than humidity gradients and temperature boundaries. If this hypothesis is accepted, then the overriding influence of temperature over humidity for limited periods in the laboratory appears reasonable. This behaviour is in marked contrast to that of the spruce budworm, *Choristoneura fumiferana* Clemens, which lives and travels on branches where moisture gradients from the foliage periphery to the trunk is gradual, but the temperature gradient from the hot periphery to the cool interior is abrupt (WELLINGTON, 1950). In the laboratory, they selected a constant evaporating gradient irrespective of changes in the temperature gradient (WELLINGTON, 1949). Thus, to spruce budworms, moisture gradients are more important than temperature gradients.

It is sometimes stated that small animals, when left undisturbed, spend a large proportion of their lives immobile. This may be particuliarly true with *B. geniculosa*, for they are normally quiescent on a rough substratum but become very active on a smooth surface. Living among the rough surfaces of the lower litter layers of the woodland, in between spurts of activity there are probably long periods of complete rest. This behaviour can readily be observed in culture cells with smooth plaster-of-Paris base, where individual mites remain still for long periods amongst the rough litter-debris. If the detritus is removed they immediately become, and stay, constantly active.

Although the mites normally live in a near-saturated atmosphere, they nevertheless avoid a moist surface when offered a dry alternative. However, in drier humidities gradual desiccation will lead them towards a moist substratum. But since a rough, moist surface is preferred to a smooth, dry one, the presence of " free " moisture in their environment is unlikely to effect their behaviour to any great extent.

The mites are usually exposed to low illuminances ; they are probably repelled by direct sunlight on the woodland floor, but may become attracted to crepuscular light. This probably engenders activity at dusk which, in addition to the lowered surface temperature and rapid rise in humidity, enables the mites to explore the upper litter layers. Since little is known of the diurnal rhythm of these mites, more work is needed before elucidating such problems. Some preliminary work (MADGE, *unpublished*) has shown, however, that they remain constantly active throughout 24 hours on a smooth surface, while on a rough surface they show a clear diurnal rhythm.

Finally, *B. geniculosa* characteristically covers its integument with its cast skins and debris from its natural habitat. This behaviour is generally confined to the pale, soft-skinned juveniles and is only rarely seen in the dark, strongly sclerotized adults. This artificial cover does not restrict excessive water-loss since the mites are covered by an impermeable waxy epicuticle that is quickly replaced when accidentally abraded. However, the exuviae and detritus may act as a camouflage against predatory mites and other enemies.

Other species of oribatid mites.

Some observations were also made on the sensory physiology of other oribatid mites living in different environment, which are summarised as follows. *Humerobates rostrolamellatus* Grandjean lives in cracks in the bark of fruit trees, clustering in small groups amongst bare patches of the alga *Pleurococcus*. The mites are thus exposed to situations with marked diurnal and seasonal fluctuations in temperature and humidity. They cluster and are inactive during daytime because the air is dry and small fluctuations are not readily detected. In prolonged dry weather, however, the mites move to deeper fissures in the bark, where humidity and temperature are more tolerable. With the sharp rise in humidity during darkness, the mites disperse and browse on *Pleurococcus*, so long as the temperature is suitable. Owing to the blanketing effect of the tree canopy, clouds, bark-scales etc., the temperature on the bark during daytime is probably cooler than expected (HAARLOV and PETERSEN, 1952).

The behaviour of clusters of *H. rostrolamellatus* in dry or moist air is readily seen in the laboratory. Batches of undisturbed mites on a fragment of bark maintained an intact cluster for at least 24 hours in dry air, but they quickly dispersed in saturated air. In dry air, a cluster of about 50 mites remained aggregated for a day at 19-21° C ; when forcibly scattered, they quickly re-aggregated. They were unable to feed on the dry *Pleurococcus* on the bark. But in saturated air, the same cluster dispersed in under 2 hours and remained constantly active. This behaviour remained unchanged after 2 days. Under these conditions, they readily fed on the damp *Pleurococcus*. *H. rostrolamellatus* survived in dry humidities for much longer periods than the other species of oribatid mites studied, and also tolerated greater temperature extremes. However, they died after prolonged exposure to moist air at relatively high temperature. There is an obvious relationship between these results and the conditions encountered in their habitat.

Details of the reactions of *Platynothrus peltifer* (Koch) are not given here since they are found in situations similar to those of *B. geniculosa* and *Fuscozetes fuscipes* (Koch) (below). However, they are more responsive to high humidities than *B. geniculosa* and this probably accounts for their occurrence in larger numbers in wet sphagnum moss than in woodland litter (MADGE, *in preparation*).

F. fuscipes lives in the " stalk layer " of sphagnum, where extreme heat and drought are unlikely to occur. Owing to the insulating canopy of the " heads " of the moss and to the heat generated by the underlying peat, the daily and seasonal fluctuations in temperature within the moss-carpet are very small. It is generally cooler than the air above during the summer and warmer than the air in the winter. Sphagnum has a high water-holding capacity and is capable of absorbing atmospheric moisture (OVERBECK and HAPPACH, 1957), hence the humidity in the " stalk layer " is always saturated (NORGAARD, 1951 ; MADGE, *in preparation*).

Laboratory experiments have shown that the humidity behaviour of *F. fuscipes* is closely related to the humidity conditions of their habitat. Mites with a normal water-balance did not respond clearly to any humidity. When desiccated, they responded feebly and chose high rather than low humidities, but the results were inconclusive. The mites soon died in dry air but survived much longer in high humidities. *F. fuscipes* possesses hygroreceptors that probably only function when the mites become slightly desiccated.

Although very widespread, certain oribatid mites are thus incapable of adapting themselves to a thoroughly terrestrial existence, the foremost characteristic of which is the possibility of existing in a dry atmosphere. Many of them are therefore condemned by the exigence of their structure and behaviour to live in a much circumscribed habitat, but some species have evolved behaviourial and physiological adaptive features enabling them to exploit a wider range of environments.

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