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# ON THE BEHAVIOUR OF PIGEON LOUSE, *COLUMBICOLA COLUMBAE* LINN. (MALLOPHAGA)

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(With 6 figures in the Text)

## INTRODUCTION

From the literature available it seems that no study has been made of the behaviour of the pigeon louse, *Columbicola columbae* Linn., nor of that of any other Mallophaga. The behaviour of the human louse, *Pediculus*, however, has been studied in great detail by Hase (1915, 1931), Bacot (1917), Nuttall (1917, 1919), Alessandrini (1919), Martini (1918), Pick (1926), Homp (1938), Buxton (1939) and Wigglesworth (1941); while Weber (1929) has given a detailed account of the behaviour of the pig louse, *Haematopinus*. The present paper describes the reactions, under laboratory conditions, of the pigeon louse to three environmental factors, namely temperature, smell and contact. The classification of the mechanism of orientation given by Gunn, Kennedy and Pielou (1937) has been followed here.

## GENERAL METHODS AND MATERIAL

The pigeon louse lives normally concealed on the surface of the vanes of feathers. It spends the greater part of its life at rest. The well-fed adult lice of both sexes were collected directly from the pigeon either at the time of performing the experiments or earlier and they were kept in a big Petri dish on the pigeon feathers. There was little difference in the behaviour of lice collected before or at the time of the experiment, but if they were collected more than a week before the experiment they became sluggish and their behaviour was not normal.

The method of experiment and the apparatus used were substantially the same as those described by Wigglesworth (1941). The metal containers used were rectangular, measuring 6 × 9 × 12 cm., the uppermost wall 6 × 9 cm. The two containers were separated by an asbestos sheet 2 mm. thick, and held together by means of an outer rubber band. The temperature of the containers could be changed to the desired degree by adding ice or by heating water inside them. The temperature was measured by a sensitive resistance thermometer. The arena was circular, glass-walled and 5 cm. in diameter. The floor was usually of paper, except in those cases in which the behaviour was studied on cloth which was stretched on a wooden embroidery frame. Except in temperature experiments the arena rested on a table and the temperature of the surroundings varied between 31 and 32 °C. In temperature experiments half of the arena rested on one container and half on another. The arena was always near the window and the experiments were performed in diffuse daylight in the morning hours.

The reactions of the louse were observed in the arena which was so arranged that one half differed from the other half in a single factor at a time. A single fresh louse was used for each test. The duration of each experiment varied from 10 to 20 min. Over this range, the duration of the experiments did not seem to have any appreciable influence on the intensity of the reaction. The tracks made by the louse during its movements on the floor of the arena were copied on a sheet of paper by the side of the apparatus, and with the aid of a stop-watch the positions of the louse were marked at 30 sec. intervals. From such tracks it was possible to compare the relative lengths of time spent by the louse in either half of the arena and to determine whether this was due to (i) coming to rest or moving more slowly to one side (orthokinetic reaction), (ii) changing direction more frequently (klinokinetic reaction), or (iii) constantly avoiding one side (klinotactic reaction). When the louse moved against the wall of the arena, its tracks were recorded, for the sake of clearness, as concentric lines.

## BEHAVIOUR IN A UNIFORM ARENA

Before interpreting the behaviour under a particular condition it was very essential to have knowledge of the movements of the louse in a uniform arena. It might be mentioned here that there were many individual variations. In some cases the louse would come to rest after moving a minute or two and would continue in this position for some time; in other cases it would go on moving in spirals and so on.

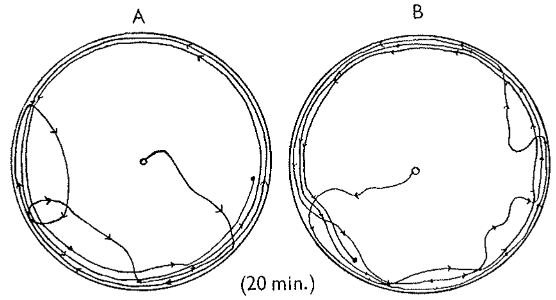


Fig. 1. Tracks followed by the louse in a uniform arena.

But generally the louse moved forward near the wall of the arena often touching the wall with its antenna (Fig. 1). Occasionally the louse crossed the arena at some distance from the wall or turned and walked back. Records were made only of the tracks of individuals showing normal behaviour, which was determined by performing a number of experiments with different individuals under each of the conditions; when a number of individuals showed a more or less similar behaviour, this was taken to be normal.

## REACTIONS TO TEMPERATURE

When the louse was given a choice between 23 and 30·5° C. (Fig. 2A), it spent nearly all its time on the warmer side and strongly avoided the cooler side. When it was introduced on the warmer side it remained there and did not enter into the



cooler side. But, on introducing it on the cooler side, it crossed the cooler side as soon as it could and entered into the warmer side, where it remained all the time. The track followed was not straight, but a little convoluted. More or less similar behaviour was observed when the alternative temperatures were 25 and 30·5° C. (Fig. 2B).

Fig. 2C shows a typical track of a louse given a choice between two extreme alternative temperatures 27·5 and 47·5° C. The louse on the warmer side moved very fast and reached the asbestos sheet, but did not enter the cooler side. It continued moving in the middle zone, taking a very irregular convoluted course. It avoided both the temperatures strongly and showed a great preference for the

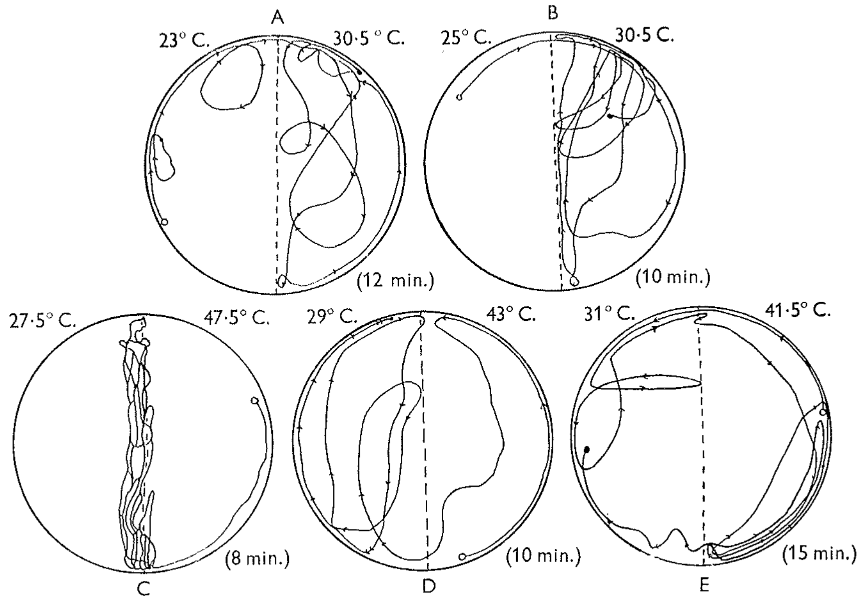


Fig. 2. Tracks of the louse when the two halves of the arena had different temperatures.

middle zone. While it was moving on the asbestos sheet, it touched sometimes the cooler side and sometimes the warmer side. This greatly confused the louse, making its course all the more erratic and the result was a very irregular convoluted track.

When these results were obtained, the response to other differences on the temperature scale was studied in order to find out how sensitive the louse was and its preferred temperatures (thermopreferendum). For this purpose the temperatures were progressively lowered on the warmer side and raised on the cooler side. The temperature differences used varied from 4 to 20° C.

Between two alternative temperatures, 29 and 43° C., the behaviour of the louse became very different. As long as it remained on the warmer side it moved very fast (Fig. 2D) and, after reaching the asbestos sheet, entered the cooler side and spent practically all the time there. This showed that the louse preferred 29° C. in comparison to 43° C., which was strongly avoided. The behaviour of the louse on the cooler side further suggested that this side was also not liked much, as it often moved towards the centre to find a more suitable place.

When the choice was between 31 and 41·5° C., a very interesting behaviour was shown (Fig. 2E). Instead of avoiding the warmer side, the louse preferred it and avoided the cooler side. However, the avoidance was not so strong as it was when higher temperatures were used. This observation further suggested that the preference to 29° C. in comparison to 43° C. (Fig. 2D) was under compulsion, as the louse had strongly avoided 43° C., so that 29° C. should not be regarded as the thermopreferendum. Again, the louse preferred 36° C. in comparison to 31° C. (Fig. 3A). This behaviour suggested that the thermopreferendum was somewhere between 31 and 41·5° C.

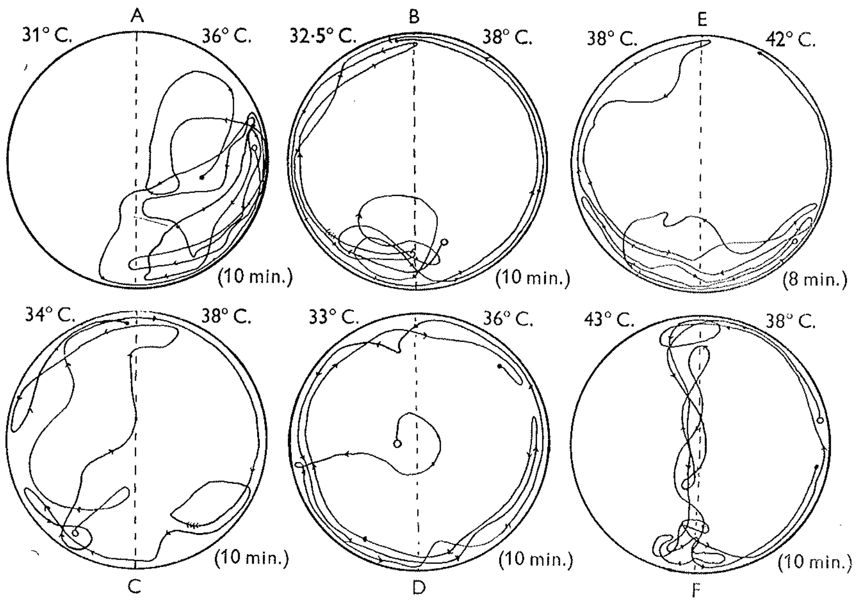


Fig. 3. Tracks of the louse when the two halves of the arena had different temperatures.

To find out the minimum range of the thermopreferendum the choice was given between 32·5 and 38° C. (Fig. 3B). The louse preferred 32·5° C. more, but 38° C. was also not avoided. Similarly, when 34° and 38° C. were used (Fig. 3C), 34° C. was preferred, but the louse could not discriminate between 33 and 36° C. (Fig. 3D). As there was a stronger preference for 34° C. than for 38° C. and the louse could not discriminate between 33 and 36° C., the thermopreferendum was between 33 and 36° C.

When the choice was between 38 and 42° C. (Fig. 3E), 38° C. was preferred, although 42° C. was also not strongly avoided; but, when the temperature was raised to 43° C. on the 42° C. side (Fig. 3 F), the raised temperature was strongly avoided, showing that at this range the louse was sensitive to a change of even one degree of temperature.

The results obtained showed that temperatures above 42° and below 30° C. were strongly avoided by the louse. 30–32° and 38–42° C. temperatures were well



tolerated but never preferred to temperatures below 38° and above 32·5° C. The preferred temperature was 33–36° C., and there was no appreciable change in the reaction of the louse to temperature differences within this range. The louse was sensitive to temperature differences of even one degree below and above the range of tolerated temperatures, two degrees difference within the range of tolerated temperatures, and three degrees difference within the range of preferred temperatures.

The tracks of the louse were much convoluted within the range of temperatures strongly avoided. Within this range the louse seemed confused and hesitant and frequently raised its head. When a louse moving on the warmer side reached the cooler side, its speed was lowered. Similarly, when it moved to the warmer side from the cooler zone, the speed increased. The maximum speed was noted at 47° C., when it covered a distance of 50 mm. in 20 sec. (150 mm. per min.). The louse did not show any signs of sensory adaptation to these adverse temperatures, because the speed remained more or less the same throughout under similar conditions.

### *Mechanism of orientation*

The foregoing experiments demonstrated that the louse avoids both high and low temperatures, and prefers moderate temperatures. It appears that at least three mechanisms of orientation contribute to this behaviour. These mechanisms are orthokinesis, klinokinesis, and klinotaxis.

When a louse is exposed to a pair of low and high temperatures in the alternative chamber, and crosses from the low to the high temperature zone, its rate of movement instantly increases. Similarly, when the louse crosses from the high to the low temperature zone, its rate of movement instantly decreases. This simple mechanism of behaviour may be termed orthokinesis.

When it passes from one zone to another the louse often does not follow a straight course, but frequently turns and changes its direction. This mechanism of orientation is known as klinokinesis.

Another mechanism seems to be at work when the two alternative temperatures are cold and hot. None of these temperatures are liked by the louse. Sometimes it moves to one side and sometimes to the other, but it avoids both the zones and remains in the middle part of the arena. This type of mechanism is a directed one and is termed klinotaxis.

It appears that all the three mechanisms are responsible for the general temperature behaviour. But it is difficult to define the exact part played by each mechanism, except in some cases. When there is the sharp avoidance of any one temperature, it may be said that it is due to klinotaxis, as in the case of high and low temperatures. This mechanism is effective in keeping the louse away from unsuitable temperatures. The increased frequency of turning may be regarded as being due to klinokinesis, the mechanism which is important in bringing the louse to preferred temperature. The change in the rate of movement appears to be due to orthokinesis, which, together with klinokinesis, may also be important in avoiding unsuitable temperatures.

REACTIONS TO SMELL

The method used for testing the reactions of the louse towards smell was roughly the same as that used in the temperature experiments. One half of the arena was so arranged as to have the smell being tested.

When one side of the arena was of untreated paper and the other of paper rubbed on a pigeon, the louse strongly avoided the neutral side. The avoidance was so strong that the louse walked almost immediately from the neutral side to the side smelling of pigeon and spent practically all the time there (Fig. 4A).

In another experiment the bottom of the arena was that of voile, and half of it had pigeon feathers underneath. The louse showed definite preference (Fig. 4B) for the side that had the pigeon feathers. The track was much convoluted, perhaps because of some confusion regarding the regularity of the smell.

When one half was neutral and the other contained paper smelling mildly of kerosene, the louse very strongly avoided the side smelling of kerosene (Fig. 4C).

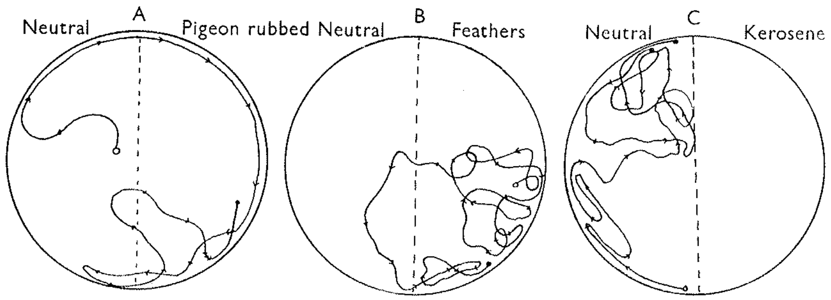


Fig. 4. A and B, reactions of the louse to the smell of pigeon feathers; C, reactions of the louse to the smell of kerosene paper.

*Mechanism of orientation*

Three mechanisms appear to be involved in orientation of the louse in relation to smell. When the louse enters the favourable side from the unfavourable side, it does not walk straight, but follows a convoluted course, although it definitely avoids the unfavourable side. Klinokinesis is responsible for avoidance of the unfavourable side and for a longer stay on the favourable side. The klinotactic mechanism keeps the louse away from the unfavourable conditions. When it is on the unfavourable side, the louse walks faster and thus is able quickly to avoid unfavourable conditions; by slowing down its movement on the favourable side, it is able to keep longer under favourable conditions. This behaviour is due to orthokinesis.

REACTIONS TO CONTACT

The same type of arena was used as before, each half of the bottom having a different surface. The materials used to make these surfaces were unglazed paper, glazed paper, blotting paper, tin foil, voile, silk and wool.

The louse could not hold on to glazed paper, which was avoided altogether.



When it was left on the glazed paper, it did not move. When it was forced to move, it had to struggle hard, its claws slipping over the surface (Fig. 5A).

When the louse was given a choice between unglazed paper and blotting paper, it preferred the unglazed paper (Fig. 5B) and avoided the blotting paper.

On tin foil the louse experienced more or less the same difficulty as on the glazed paper and preferred even blotting paper to tin foil (Fig. 5C).

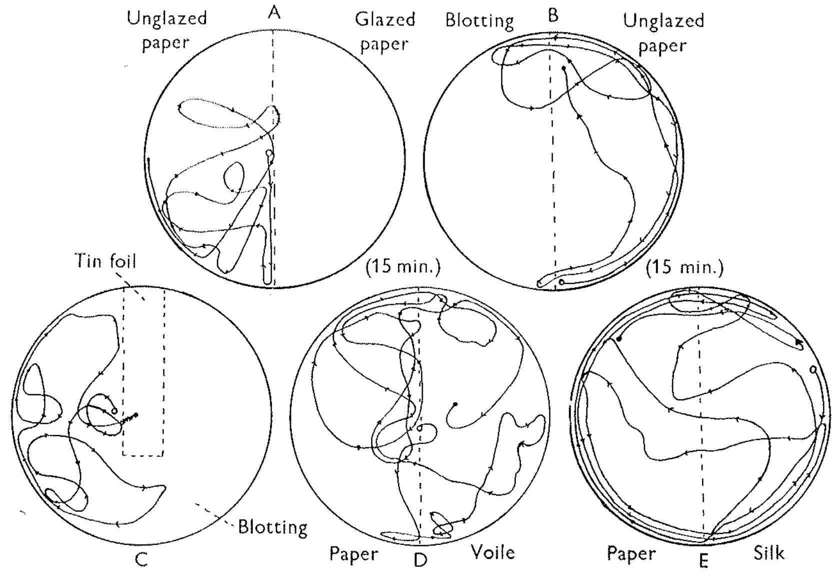


Fig. 5. Reactions of the louse to contact when the two halves of the arena had different surfaces.

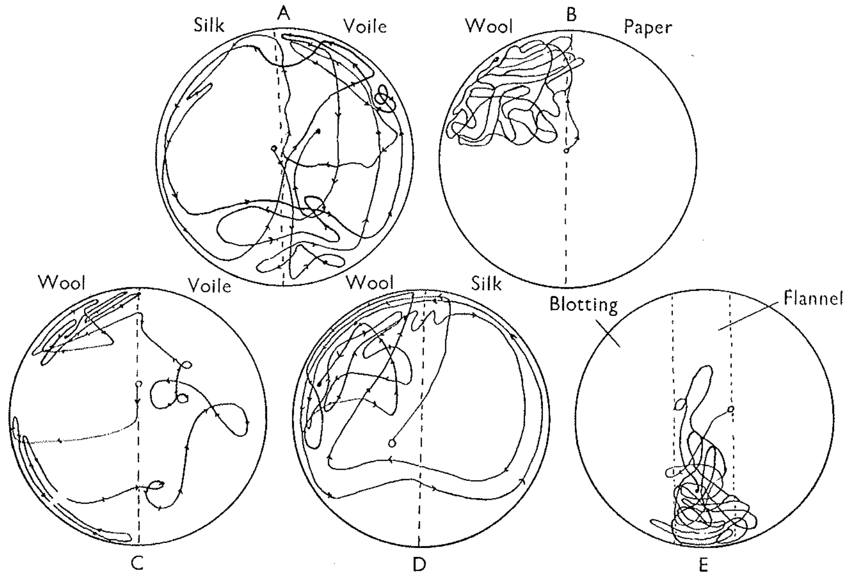


Fig. 6. Reactions of the louse to contact when the two halves of the arena had different surfaces.

When the choice was between voile and unglazed paper (Fig. 5D) or paper and silk (Fig. 5E), the louse preferred the paper, but there was no avoiding reaction towards voile or silk. The louse did not show much discrimination between silk and voile (Fig. 6A).

When the louse was offered paper and wool, it avoided paper strongly (Fig. 6B). On a woollen surface it took a much convoluted course and, when it happened to reach the paper surface, it returned to the woollen side immediately. In the case of wool and voile (Fig. 6C) or wool and silk (Fig. 6D), the preference was again for the woollen surface. Thus the louse showed a strong avoiding reaction towards paper, silk and voile, when the alternative material was wool. It also preferred a frayed strip of flannel to blotting paper, which was then strongly avoided (Fig. 6E).

### *Mechanism of orientation*

The mechanism of orientation to contact appears to be the same as that to other stimuli. Orthokinesis comes into action when the louse moves on paper, voile and silk, on which it walks more actively than on other surfaces. On a glazed surface the louse is unable to walk and comes to rest; this sort of mechanism may be called as negative orthokinesis. On a woollen surface the louse follows a very convoluted track and the mechanism involved appears to be klinokinesis. The distinct avoidance of silk, paper and voile, when the alternative material is wool, is probably due to klinotaxis.

## COMPARISON OF THE BEHAVIOUR OF THE PIGEON LOUSE AND THE HUMAN LOUSE

Wigglesworth (1941) has given a detailed account of the behaviour of the human louse and has critically reviewed the literature on this topic. The human louse and pigeon louse belong to two different Orders, but they show similarities in many respects and a comparison of their behaviour is therefore of interest.

The behaviour of both human and pigeon lice is more or less similar in a uniform arena; they generally move near the wall, often touching it with their antennae.

Both human and pigeon lice show thermo-klinotactic, thermo-klinokinetic and thermo-orthokinetic mechanisms of orientation. The thermopreferendum for the two lice depends on the body temperatures of their respective hosts. For the human louse the recorded thermopreferendum is about 30° C. the human body temperature being about 37° C. Similarly, the thermopreferendum for the pigeon louse is about 35° C., the pigeon body temperature being about 42° C. Thus for both the lice the thermopreferendum is about 7° C. below the body temperature of their respective hosts.

A comparison of the tracks of both the human and pigeon lice at different combinations of two alternative temperatures further reveals that their behaviour is very similar to the temperatures below and above their respective thermopreferenda. It may be pointed out that the behaviour of the two lice appears to be more or less similar when the temperature difference within their thermopreferenda is the same.



The rate of movement of both the human and pigeon lice is always greater on the warmer side; and no good evidence of thermoadaptation by either louse has been found.

Both the human and pigeon lice are sensitive to the odour of their respective hosts. The human louse shows a definite preference for cloth worn by man for a few days; and the pigeon louse prefers cloth rubbed on a pigeon to neutral cloth.

Neither the human nor the pigeon louse can hold on to glazed paper. When they are forced to walk on glazed paper they have to struggle hard, their claws slipping over the surface. They show a preference for woollen cloth in comparison with unglazed paper and their tracks are then more or less similar in that they follow a convoluted path. They also prefer woollen cloth to cotton. In the case of cotton and silk the pigeon louse shows a definite preference for voile, while the human louse appears to avoid cotton stockings. Their behaviour on frayed flannel is also similar.

## SUMMARY

The reactions of the pigeon louse *Columbicola columbae* to temperature, smell and contact have been tested in a circular, glass-walled arena divided into two halves. The thermopreferendum has been found to be between 33 and 36° C., and higher temperatures are more strongly avoided than lower ones. The louse prefers cloth that has been in contact with pigeon feathers to clean cloth. Kerosene serves as a repellant. When the louse is offered different surfaces, namely, glazed paper, tin foil, blotting paper, unglazed paper, voile, silk or wool, the woollen surface is preferred most.

Three mechanisms of orientation, klinotaxis, klinokinesis and orthokinesis appear to contribute to the normal behaviour of the louse. Under certain conditions negative orthokinesis also affects the behaviour.

Comparison of the behaviour of the pigeon louse and human louse has shown that in many respects their behaviour is similar and that their thermopreferendum depends on the body temperatures of their respective hosts.

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