The ecology of Columbicola columbae L. (Mallophaga)

by

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I. Introduction

The ecology of the Mallophaga is a comparatively unknown field of research. It is true that ecological problems of this insect group have been investigated, but usually these studies have been limited to problems associated with specific growth and bionomics. The investigations are also often restricted to those Mallophaga which are important from an economic point of view and, consequently, several authors have studied the same few species, leaving most genera and species uninvestigated. A complete list of the investigations published to date is given below. As regards the nomenclature of the species discussed in this paper, I refer to the checklist by Hopkins & Clay (1952).

I wish to express my deep gratitude to Professor Carl H. Lindroth, the head of the Entomological Department of the Zoological Institution in Lund, where this work was performed. His interest and support have considerably facilitated the investigation. I am also indebted to Dr. Per Brinck, Zool. Inst., Lund, for his willingness to discuss the results and the problems arising, and to Dr. Theresa Clay, British Museum, London, who has allowed me to utilize her knowledge of the literature on the Mallophaga.

II. Previous investigations

Our present knowledge of the bionomics and ecology of the Mallophaga is based chiefly upon observations on reared material. The methods of rearing have been of two kinds.

1. The Mallophaga have been cultivated on their hosts, either free or enclosed in a box. For practical reasons this technique is mostly restricted to species living on mammals. It has been used by the following authors: Lamson (1917) (Damalinia bopis L., sub nom. Trichodectes scalaris Nitzsch), Schull (1932) (Damalinia bopis, sub nom. Bovicola b.), Ewing (1924) (Gyropus ovalis Burm. and Gliricola porcelli Schrank), Dubinin (1948) (Piagetiella titan Piaget, sub nom. Tetroptthalmus t.).

2. The Mallophaga have been cultivated under artificial conditions in an incubator with constant temperature and humidity. Since the specimens are thus easier to observe, these investigations were often more exhaustive than the former. The technique has been used by Osborn (1890) (Dennyus hirundinis L., sub nom. Nitzchia palicare auct.), Oudemans (1912) (Falcolipeurus quadripunctatus Giebel, sub nom. Lipeurus q.), Barber (1923) (Brüelia vulgaris Kellogg, sub nom. Nirmus v., and Philopterus citrinellae Schrank, sub nom. Docophorus communis Nitzsch), Martin (1934) and Eichler (1936 a, 1936 b, and 1937) (Columbicola columbae L.), Wilson (1934) (Cucletogaster heterographus Nitzsch, sub nom. Lipeurus h., Menopon gallinae L., and

Opusc. Ent. 1956, XXI: 2–3

Many of the papers listed above are very short and give rather scanty information. Some of the species mentioned have only been recorded as difficult or impossible to rear.

III. Material

Columbicola columbae was chosen as the subject of my work because, according to Martin (1934), Eichler (1936 a and b), and Conci (1952), this species seems to be easily reared and thus well suited to an investigation of the ecology, which had not been closely studied before.

The specimens used in my experiments were either reared in an incubator or taken directly from domestic pigeons. Both groups showed the same reactions. About 400 specimens from about 25 pigeons from Scania in southern Sweden, were studied in the present investigation.

On collecting the biting lice I found that white pigeons were more heavily infested with Mallophaga than others. Thus these pigeons seem to be less resistant to infestation, probably owing to a weaker constitution. According to information from their breeder they are also more difficult to rear.

IV. Methods

In breeding the Mallophaga I have adopted the technique previously used by Martin (1934), i.e. a standard incubator which, however, was completed with a more exact heating control and a fan. The temperature was kept at 34.5° C. and the relative humidity at 90%. The specimens were reared in glass dishes containing feathers from the wings and back of a pigeon. It proved suitable to cover the bottoms of the dishes with a layer of chopped feathers, and the cultures with glass slides in order to protect them from dust and spores of mould. By this method several generations of Columbicola columbae were reared without difficulty.

The species' reactions to temperature were studied in an alternative chamber constructed according to the same principles as the apparatuses used by, among others, Graber (1887), Thomson (1938), and Wigglesworth (1941). Special problems, however, are involved with Columbicola columbae, as this species did not move normally on an artificial stratum. Thus only a feather could be used, which made it difficult to avoid vertical temperature gradients.

Opusc. Ent. 1956, XXI: 2–3
Fig. 1. Alternative chamber used in the temperature experiments with *Columbicola columbae* L. A heating tank (with an electrical immersion heater), B cooling tank with pipes for inflowing D and outflowing water E, C insertion with a feather held by two uprights. (Measurements in cm.)
in the chamber. I also intended to make the temperature difference between the two halves as great as possible and therefore the apparatus was constructed as shown in fig. 1. It is made of plexiglas and the heating and cooling apparatuses completely enclose the two halves of the chamber. The heating apparatus around the warmer part is a tank filled with distilled water (A). The tank is open at the top where a mixer and an electrical immersion heater with a regulator are placed. On the side facing the other tank (B) is pasted a paragum plate with an aperture cut out just over the depression designed for the insertion (C) but some mm larger than the depression. The tank around the cooler half (B) is closed except for three pipes for out- (D) and inflowing (E) tap-water and for a thermometer. During my experiments the tank has been used in this way but, if necessary, it can be modified to allow higher temperatures in the cooler part of the alternative chamber. The bubbles of air precipitating on the inner walls are easily removed by adding to the water a substance, which lowers the surface-tension. Since the roof of each tank is slanting, all bubbles will pass out with the outflowing water without making observations difficult. The roofs of both tanks being of a step-like construction, the observations are not hindered by any water reflections.

The bottom of the insertion (C) is circular, with its margin turned up so that it can contain salt solutions controlling the relative humidity. The wall separating the two halves has a very narrow, horizontal slit round the feather and is made of three closely joined rectangular slides. The middle one is somewhat larger than the lateral ones and corresponds exactly to the aperture in the paragum plate pasted on to tank A. The two lateral slides are of equal size and when the tanks are put together they project some mm into

Fig. 2. Observation chamber. A container for the Mallophaga. B heating-windings, C temperature regulator with circuitbreaker D. E glass slide with electrical heating, F transformer, G microscope.

*Opusc. Ent.* 1936, XXI: 2–3
the depressions in the tanks designed for the insertion. This construction restricts the heat exchange between the halves to the narrow slit. The paragum plate completely prevents any communication with the environments.

If the apparatus is used as a circular arena for insects which are able to walk on an artificial ground, such a stratum can be placed over the circular bottom and a horizontal slit can be cut out just over it in the separating wall. During nearly all my experiments, however, the feather was placed perpendicularly to the separating wall and held by two uprights.

Provided the temperature of the running tap-water in tank B is kept constant, the apparatus will maintain the different temperatures in the alternative chamber without any attention from the observer. During all the experiments the RH was kept at 75 % by means of a saturated solution of sodium chloride. The illumination was diffuse and dim.

The specimens of Columbicola columbae did not seem much disturbed by the experimental conditions, which was proved, inter alia, by the fact that they often copulated during the experiments. The results must therefore be considered as closely corresponding to the normal reactions of this species.

It is not evident from previous papers concerning the bionomics of Mallophaga whether the observed specimens have been studied under optimal circumstances (temperature etc.). For my own observations a chamber of plexiglas was constructed in such a way that the temperature was automatically regulated and the specimens could be continuously observed through a microscope (fig. 2). Since the Mallophaga are sensitive to heatrays a common fluorescent light tube was used as a light-source instead of an electric bulb. In spite of this precaution the specimens probably became irritated (cf. Wundrig 1936). The RH was 75 %.

All the present photographs have been taken by flash-light and the insects have not been prepared in any way.

V. Biology

On a pigeon. Columbicola columbae are normally found on the under wing-coverts and the proximal part of the remiges. They are seldom found on the body. It is a general rule in the Ischnocera that the species of the flattened elongated type (like Columbicola) inhabit the wings, whereas the short, round-bodied species are characteristic of the head, back, and throat (Dubinin 1948, p. 195—196; Clay 1949, p. 280; Blagoveshchenskii 1950, p. 106).

The individual biology has already been closely investigated by Martin (1934), and another investigation by me would probably mean only confirmation of her observations. Martin never observed the species to feed on anything other than the barbules of the feather, except in one case, when a larva fed on a drop of blood. This specimen died two days later. At copulation the position of the male is underneath the female, as is usual in the Philopteridae. The pterothorax of the female is clasped just in front of the coxae of the hind legs by the male with his antennae. The male curves the end of his abdomen up to meet hers. Martin’s paper deals furthermore with oviposition and hatching, with excellent tables of the duration and length of the different instars. The ecology was not investigated. Martin’s records of feeding habits have since been supplemented by Eichler (1936 b, 1937). Un-
like Martin, he never saw the species feed on blood. A close study of the digestion has been made by Waterhouse (1953). The copulation has also been thoroughly investigated by Schmutz (1955) from an anatomical point of view. The reaction to light has been studied by Wundrig (1936) who found the species to be “negatively phototactic”.

VI. Results

a. Reaction to temperature

The following experiments to determine the autoselected temperature were carried out by means of the alternative chamber. At the beginning of an experiment, five specimens were put on each of the basal and apical portions of the feather and their final positions were registered. The specimens did not settle until after the first hour, whilst there were no evident differences between experiments lasting from two to twelve hours. According to this, three hours was chosen as standard time for the experiments, which therefore probably give significant results without being uncomfortably lengthy.

In all, the reactions of 300 Columbicola columbae have been noted. The experiments can be classified into three groups, each of them consisting of 100 specimens:

1) Basal portion of the feather in 17° C., apical portion in 35° C.
2) Basal portion in 35° C., apical portion in 17° C.
3) Whole feather in 35° C. (control group).

The reactions of the three groups are given as histograms in fig. 3 (in all the figures the feather-base is on the left).

The results of the three groups have one feature in common: the specimens show a pronounced accumulation on the basal portion of the feather. The majority of them always settle on this part: at the end of the experiments, altogether 262 specimens = 87% were found there. The accumulation is greater close to the quill and decreases distally. The reason for this will be discussed later on. On the other hand, the specimens are not at all influenced by temperature when orientating on the feather. As a matter of fact they have not been attracted by either of the alternative temperatures although that of the warmer part (35° C.) is close to their supposed optimal temperature, that is the temperature of their host (cf. Martin 1934, p. 7). The difference in temperature was 18° C., which should have been detected by the Mallophaga had they been at all sensitive to temperature within the limits used.

A closer comparison of the three groups gives some interesting details (fig. 3 B). According to my observations (vide p. 181), the specimens migrate to the base of the feather when irritated. The accumulation would consequently be closer towards the base if they were more irritated by the cooler temperature (17° C. — group 1) than by the more optimal one (35° C. — group 2). However, such an effect cannot be proved and the specimens seemed to have no temperature discrimination within these limits.

Furthermore, during the experiments with alternative temperatures
Fig. 3. Position of *Columbicola columbae* L. in the experiments with alternative temperature.

A Primary results. Each histogram shows the summarized result from one of the groups. The vertical lines represent the number of specimens on each mm of the feather.

B Mean values of 5 mm.

*Opusc. Ent. 1936, XXI: 2--3*
(groups 1 and 2), there is a less accentuated accumulation in the proximity
of the slit between the two halves of the alternative chamber. Owing to the
great difference in temperature there must be a marked circulation of air in
this slit. When exposed to streaming air these insects immediately stop
moving and press up against the vane (vide p. 187). Consequently they gather
close to the slit. As these Mallophaga chiefly move towards the base of the
feather, the accumulation becomes greater on that side. Such an accumulation
is not found in group 3, apparently because no air circulation occurs through
the slit (fig. 3 B).

Finally some supplementary experiments have been carried out. During
two of them the warmer part was 32°C. only and the cooler part still 17°C.
Some experiments were prolonged to eight and twelve hours. The reactions

Table 1. Position of Columbicola columbae L. in an experiment with
alternative temperature. The insertion was reversed every hour.

<table>
<thead>
<tr>
<th>Hours</th>
<th>Basal half °C.</th>
<th>Slit Number of specimens</th>
<th>Apical half °C.</th>
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<tr>
<td>0</td>
<td>35</td>
<td>5</td>
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<td>1</td>
<td>35</td>
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of the Mallophaga were still the same. During one experiment the insertion
was reversed every hour without removing the material. No reaction to
temperature could be observed (the results are given in table 1). It is note-
worthy that the number of specimens gathering at the slit increased during
the experiment. The reason why no specimens at all were found on the apical
portion of the feather is probably the fact that they became irritated when the
insertion was reversed. Some artificial strata have also been tried (different
kinds of cloth and paper) with alternative temperatures of 40—36, 35—30,
32—27, and 18—34°C. In all, the reactions of 65 specimens were noted
during these experiments. They still showed no response to temperature.

Thus, in contrast to what has been previously considered regarding the
Mallophaga, at least Columbicola columbae has no thermokinetic or -tactic
reaction underlying a positive reaction to the body of their host.

The species has also been tested at 45°C. In these experiments the base of
the feather was all the time in the warmer part of the alternative chamber.
The tendency to migrate to the base remained quite obvious but in 45°C. the
specimens became extremely excited and ran about very quickly, making
frequent turns. On reaching a more tolerable temperature their activity de-
creased and so they agglomerated as close to the base as they could stand,
i.e. in the slit. Some specimens maintained the usual behaviour, migrated to the base and were killed by the heat. Their movements in 45°C were undirected and their reaction can be classified as klinokinetic.

It is thus evident that a response to high, lethal temperatures can be connected with lack of susceptibility to temperatures approximating that of the host.

Investigations of the reaction to temperature of the Mallophaga have previously been made by four authors. Barber (1923, p. 393) placed some specimens of Brüelia vulgata Kellogg in "a chamber which had a temperature of 48°C at one end and 35°C at the other" and they "migrated from the higher to the lower temperature at a rate of 4.5 cm. in eighteen hours". He also remarked that in 48°C "they showed marked irritation and all died within a few hours, while the controls lived for weeks at 35°C." Thus their reaction was probably thermo-klinokinetic and ought to be compared with the reaction of Columbicola columbae at 45°C. No more experiments were reported in Barber's paper so nothing can be stated about the response in Brüelia vulgata to the temperature of the host.

Eichler (1936 b, p. 480) put a newly killed pigeon in a refrigerator. The Mallophaga of the bird then migrated to its body. Afterwards he took the pigeon out in the room and then the insects moved to the top of the feathers but returned to the body when a heater was placed underneath it. Eichler did not mention what species had been observed. As I have repeated the experiment and Columbicola columbae, at least, did not react like that, Eichler's observations might have been made on a different species (perhaps an Amblycera).

Bair (1950) determined the autoselected temperature in Cuculotogaster heterographus Nitzsch. This was found to be 42°C, which seems rather high. Wilson (1934) reared the same species and noted (p. 304): "... the most satisfactory temperature was found to be between 33°C and 34°C". The species has also been investigated by Conci (1952) who found both the autoselected temperature and the optimal temperature for rearing to be 35—36.5°C. Martin (1934) says about Columbicola columbae at 42°C (p. 7): "Oviposition occurred infrequently... and the resulting nymphs died within a few days after hatching". Barber (1923) noted about Brüelia vulgata (p. 394): "The optimum temperature is evidently about 35°C.". Matthysse (1944, p. 437) and Scott (1952, p. 63) studied biting lice on mammals and found that temperatures above 39.5°C are unfavourable. Comparing these figures with those found by Bair I cannot consider his results applicable to normal conditions. His experiments were made without any humidity control and the conditions may have been unsuitable to the insects in this and other respects.

Conci (1952) has determined the autoselected temperature in some species of Mallophaga. This temperature was found to be 39°C in Menapon gallinaceae L., 42°C in Menocanthus cornutus Schömer. 37.5°C in Gonioodes gigas Tasch., 35.5—36.5°C in Cuculotogaster heterographus, and 36—37°C in Columbicola columbae. Conci's statement that Columbicola columbae prefers a certain temperature is quite contrary to my result that the species has no temperature susceptibility at all. I cannot explain this discrepancy, especially as Conci does not give any closer description of his experiment with this species. The number of specimens used during the experiments is only reported as regards Cuculotogaster heterographus, where only eight specimens

*Opusc. Ent. 1955. XVI: 2—3*
were utilized. Perhaps the same number of *Columbicola columbae* was used, which cannot give a significant result, whereas, on the other hand, my result is based on observations of more than 375 specimens.

An attempt will be made in the last section to discuss the temperature reactions in the Mallophaga.

**b. Orientation**

The Mallophaga constitute an insect group very well adapted to ectoparasitism. Especially the Ischnocera are closely specialized to the life on a host and so the behaviour of *Columbicola columbae* seems to be strongly influenced by the plumage qualities of the bird. The species reacts according to a highly specialized and very restricted scheme and the movements of the specimens depend strictly on the structure of the feather. Their orientation can be divided into three reactions:

1. Almost without exception they keep their bodies parallel to the barbs (rami). If they are placed on the vane at an oblique angle to the barbs, they will soon change position. This behaviour is probably due to the fact that the barbs rise over the surface formed by their barbules (radii). Parallel scores,
Fig. 5. *Columbicola columbae* L. on a piece cut out of the vane. The specimens keep parallel to the barbs with their heads turned towards the side where the shaft has been situated. Migration towards the proximal end of the vane, on the photos shown from left to right.

The bottom specimen on the middle photo is in position of repose. (B. Åkesson phot.)

e.g. engraved into a wax plate, release just the same reaction. This mode of orientation consequently depends upon the direction of the barbs and the remaining parts of the vane are without importance.

2. The specimens also direct their heads towards the shaft of the feather (fig. 4). Placed in another direction they turn immediately. This mode of orientation might seem to be connected with the foregoing but is hardly so, according to the following observation. Specimens placed parallel to the barbs but with their heads directed from the shaft (i.e. at 180° to the normal position) remain longer in this position than specimens placed in other directions. Sometimes such a specimen walks a short distance with its head in this abnormal position (still keeping parallel to the barbs), whereas a specimen placed at an angle to the barbs always turns its head towards the shaft before moving. The two reactions therefore probably depend upon different reflexes.

This mode of orientation is quite independent of the shaft itself; thus the insects keep the same direction on a small piece cut out of the vane (fig. 5). This fact is also shown by another illustrative experiment, where the vanes on both sides of the shaft were cut off, turned 180° and were again pasted to the shaft. Thus the feather looked quite normal to the human eye but the Mallophaga were still able to distinguish the original directions and consequently turned their heads from the shaft (fig. 4). Even on a single barb the specimens are able to discern the end that was originally nearest the shaft. It is of no importance whether the barb originates from a contour or down feather.
These facts show that the structures important to the orientation of the Mallophaga must be sought in the barb with its barbules which ought to be different in some directions i.e. polarized. If the polarity were perpendicular to the barb, the right and left halves of the vane should have to be different and the Mallophaga asymmetrical. This possibility does not seem very probable. On the other hand the barb may be polarized longitudinally. Such a polarity is easily found since the barbules are fastened at an oblique angle to the barb so that the proximal ends of the barbules are directed towards the shaft of the feather (fig. 6 A). Furthermore, the specimens find their way only by means of the barbules belonging to the same barb. As was just mentioned, these barbules converge towards the shaft i.e. in the same direction as the insects turn their heads. Thus the Mallophaga do not take any notice of the system of barbules between two bars, which barbules converge towards the outer margin of the vane. That the specimens distinguish the barbules belonging to the same barb only, is due to the fact that the barb forms a ridge over the surface of the barbules. This was demonstrated by placing some of the Mallophaga on a negative plastic cast of the feather. On this cast the barbs form depressions and the barbules between them elevations, and consequently the insects turned their heads from the shaft i.e. at 180° to their normal position.

When moving, the specimens keep their typical position parallel to the barbs, i.e. walking forward along a barb but more or less sidewards when moving at an angle to the barbs. It is only exceptionally that they move straight backwards.

Only one paper has previously dealt with this behaviour. Eichler (1936 b, p. 472—473) wrote about the Ischnocera: “Sie vermögen sich aber doch verhältnismässig behende auch rückwärts und seitwärts zu gehen, wobei sie auf der Feder ihren Körper meist senkrecht zu den Rami halten (schaftparallel)”.

The illustration to this statement is represented by a Columbicola columbae on a feather (I.c. Abb. I, p. 472). However, contradictory to the text, this illustrated specimen is parallel to the barbs, as in my observations. Probably the error in the text is only a lapsus calami. Nevertheless, the illustration is atypical since the specimen keeps its head turned from the shaft, which is rare. Very important is, however, that Eichler attributes the specialized orientation to all, or at least nearly all, the Ischnocera.

3. The majority of the specimens are found on the basal part of the feather (fig. 3). If they get irritated, nearly every specimen on the vane will migrate to the base usually following one of the routes shown in fig. 6 B (still keeping their bodies parallel to the barbs). On reaching the base they usually retire a short distance, return to the base, perhaps retire again etc. Finally they settle down near the base.

This behaviour is influenced neither by the shaft of the feather nor by the body of the host (fig. 5). The remaining possibility is that some quality of the vane allows the Mallophaga to discern which end of the feather is directed towards the host. There are two conceivable alternatives. Either the vane changes from apex to base, that is to say the whole feather is polarized (e.g. morphologically or chemically); or each barb is perpendicularly polarized i.e. almost in the longitudinal direction of the feather. A simple experiment was made in order to test the first possibility. The apex of a feather was removed and the rest was divided transversally. The apical and basal
portions were exchanged and were put together again so that the original base is now placed in the middle of the feather and borders on the originally apical end. By manipulating the vane the hooks will be brought to interlock, leaving no interruption in the vane. If a feather were entirely polarized the Mallophaga ought to settle at the original base. No such gathering was observed, however, but the specimens accumulated at the “new” base.

Fig. 6. Feather of pigeon (schematic). A shaft with two barbs and a few barbules. B migration of *Columbicola columbae* L. to the base of the feather. C cross-section of five barbs with their barbules demonstrating the structures important to the orientation.

According to the second alternative, all barbs would be equal and each perpendicularly polarized. As the barbules directed to the apex support the hooks and also are more extended, such a polarity is easily found. However, these structures appear in different ways at the upper- and underside of the vane, while the structures which would enable the Mallophaga to orientate have to be equal on both sides. Such a structure is formed by the grooves between the barbs on both sides of the vane, these grooves having a triangular cross-section. On the underside (= the side facing the body or downwards on the wings) such a groove is formed principally by one barb + the barbules going out from the barb following apically next to it, which barbules are directed towards the base. On the overside of

*Opusc. Ent. 1926, XXI: 2–3*
the vane a groove is formed by one barb + its own barbules on the apical side (fig. 6 C). A feature common to the grooves on both sides is that the borders turned towards the base are steep but those towards the apex gradually ascending. However, it is not quite evident whether this structure really constitutes the stimulus inducing the Mallophaga to discern the proximal end of the feather. The specimens walk so rapidly that it has proved impossible to analyze the single movements and make them coherent to the structures of the feather. Sometimes the specimens are found in a position of repose (fig. 4), usually attached to the vane by their mandibles. Their bodies are lifted up over the vane by the legs while their heads rest on the bottom of a groove. One of the lateral margins of the head is placed so close to the steep border of the groove that the antenna must be turned backwards. The antenna of the other side, however, is kept straight outwards. In this position the insects may discern the direction of the feather by the structure mentioned above. It is possible that the same structures are perceived when they move about.

A closer analysis of the behaviour of *Columbicola columbae* from a physiological point of view falls outside the scope of this paper. As is evident from the above account, the base of the feather is not the source of stimulation, although the Mallophaga migrate towards it. Instead of this, every single barb stimulates the insects laterally at one side. The movements induced are directed towards the external stimulus although the longitudinal axis of the insects is at a right angle to it. Thus the Mallophaga move from one barb to the barb next to it basally, which probably acts as a stimulus in just the same way and with the same intensity. Finally they reach the last barb at the end of the vane, where they either remain or return in the direction of the apex. Those returning soon respond, however, to the stimuli of the barbs so that they stop and return again to the base or they remain in its proximity. The migration to the base becomes less pronounced when the insects are left undisturbed.

Finally another feature will be added to the orientation described above. Most of the Mallophaga are found on the underside of the feather. It is true that they move round the edge of the vane quite freely and walk as rapidly on the overside as on the underside, but the latter is preferred. On the underside, furthermore, the specimens are more commonly found in a position of repose and their direction parallel to the barbs is more evident. Probably this side is chosen because its barbs are more elevated above the vane, thus giving better protection to the insects and facilitating their orientation.

Evidently the specimens orientate according to mechanical stimuli but it proved impossible to find out what organs are concerned with the perception. Elimination by painting or amputating the antennae, mouthparts and each pair of legs respectively had no effect on the orientation. Judging from my own experience of their way of moving it might be supposed that the median and hind pairs of legs together are concerned with the reception of stimuli. I was, however, unable to prove this hypothesis since the specimens were not able to move normally at all when these legs had been painted.

To summarize, the orientation of *Columbicola columbae* on a feather depends upon its responses to the structures of the vane. The direction of the barbs determines the direction of the longitudinal axis of the insects. It is, however, not only the qualities of the vane in its entirety which are important but also the structure of the single barb. Every barb is longitudinally as well
as transversally polarized. The longitudinal polarity releases the reaction of the individual to direct its head towards the shaft and the transversal polarity induces migration towards the base. In addition the Mallophaga prefer the underside of the feather. When observed on a living pigeon their behaviour has certainly been previously interpreted as a positive response to the temperature of the host. The eggs are laid close to the shaft on the underside of the basal part of the feather, i.e., where the imagines usually dwell.

The above discussion shows how closely the behaviour of *Columbicola columbae* depends upon the structure of the feather. Its reactions are very uniform and seldom modified, which is possible only in such a stable habitat. On a living host the migration to the base has the same result as a positive reaction to the temperature of the host. Both reactions would bring the specimens closer to the body of the host with its more optimal conditions. As could be expected, the immutability of their reflexes sometimes causes an irrational result, for instance when some specimens migrated to the base of the feather although the heat at this end was so strong that they were killed.

c. Locomotion

Previously the locomotion has been investigated in only one species of Mallophaga viz. *Strigiphilus cursor* Burm. (*Docophorus communis* auct.) (Snodgrass 1899, p. 150—153). This species moved the two legs of each of the middle and hind pairs synchronously but the two pairs moved in opposite directions. The forelegs "do not move synchronously with either of the other pairs nor with each other" and "they appear mainly to guide the body". Snodgrass added that at times the movement "becomes very much obscured and is generally more or less so". In *Columbicola columbae* I have found no synchronization either between the legs of a pair or between the pairs. *Columbicola columbae* also appears to guide the body with the fore legs. The orientation is, however, not influenced by an amputation of the fore legs. This pair of legs supports the feeding process, as was also found in *Brüelia vulgata* by Barber (1923, p. 394) and in *Cucloctogaster heterographus* by Wilson (1934, p. 308). The movements of the middle and hind legs are very rapid and "nervous" as if they are "feeling" the vane. It is possible that these legs are concerned with the tactile perception.

d. The migration to the bird's head

It is well known that when a bird has died most of its Ischnocera migrate to its head to remain there. This behaviour has long puzzled scientists working with Mallophaga. However, a simple explanation of this behaviour is suggested by the specialized orientation dealt with in the previous part of this paper.

The bird's head in itself has no attraction for the insects, which is demonstrated by the following experiment. From the back of a newly killed pigeon a rectangular piece of skin was cut out, having an area of feathers of 8.5 cm (lateral margins) × 6 cm (apical and caudal margins). Fifty specimens of *Columbicola columbae* were placed evenly spaced over this square and left for 24 hours in room conditions. Then the position of the specimens was fixed by placing the piece of skin in CO₂ and afterwards in ether. Twenty-
eight specimens (=58 %, provided all specimens survived) were registered on the nine feathers which were fastened nearest the margin originally directed towards the head of the pigeon (the whole piece of skin having more than one hundred feathers). This margin was characterized by the fact that all the feathers directed their quills towards it and their apices from it. Thus the insects migrated in the direction indicated by the quills. On the body of a pigeon all feathers have their quills placed in one direction only, viz. towards the bill of the bird. Just as in the experiment mentioned above, this is the reason why the Mallophaga migrate to this part. The migration may occur in the following way.

When the specimens get very irritated they do not only migrate to the base of the feather but continue out along the quill and try to leave it, which can be observed on a loose feather. The death of the host seems to cause such a discomfort (cf. Eichler 1936 b, p. 479) but what irritates the insects is unknown. On leaving the feather the specimens will reach the skin of the host. Since the specimens of Columbicola columbae usually move forwards and all the quills are directed towards the head the result is that they approach it. Of course they come across further quills and probably enter them but as soon as they reach the vane they will change direction and move downwards, finally returning to the body of the host. In this way the feathers always conduct the specimens towards the bird's head. There the migration is made easier because the feathers are small, lying close together so that the specimens move on the surface of the plumage. The plumage thus has the same qualities to the insects as a single feather and the bird's bill would then correspond to the quill. Perhaps an equal effect is caused on the whole body by the feathers falling together when the muscle tonus ceases after the death of the bird. Of course, all the parasites do not reach the head of the bird; some of them remain in the plumage of the body.

However, it has not yet been established whether the above results are applicable to all Ischnocera, and it should be pointed out that probably they do not hold good at all when the Amblycera are concerned.

Columbicola columbae is not a typical example of Mallophaga accumulating on the head because the species usually inhabits the wings and more seldom the body of the bird and probably only a few specimens pass from the wings to the body after the bird is dead. These specimens, however, migrate to the head where they will be found.

Previously other explanations have been put forward for the accumulation on the head. According to one of them the Mallophaga need liquid which is found around the eye of the bird. Eichler (1937, p. 99. 1952 b, p. 10) has outlined another explanation, viz. that the Mallophaga, like several other insects, climb upwards when irritated. As a shot bird is commonly held by its head the Mallophaga migrate to the head. According to my own observations, the insects accumulate on the head quite independently of the position of the host. Anyhow the behaviour of Columbicola columbae is not influenced by up and down, which can be shown by the following experiment. Twenty equal feathers were used, ten of them fastened with their quills upwards and ten with their quills downwards. One specimen was placed at the apex of each feather. The position of the specimens was registered after 15, 30, 45 and 60 minutes. The majority of the insects migrated to the feather-base and no differences in behaviour concerned with the direction of the feather could

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be observed (fig. 7 A). In a second experiment the specimens were placed at the base of the feathers and their position noted at the same intervals. Most of the specimens remained at the base (fig. 7 B).

Fig. 7. Position of one specimen of *Columbicola columbae* L. on a feather showing the independency of the migration towards the base with regard to the direction of the feather. In the figure the results from groups of ten feathers have been represented together. Observations at 15 min. intervals. The specimens have been placed A on the apices, B on the bases of the feathers.

As stated above (p. 184), the migration to the base has the same advantages for these Mallophaga as if they were attracted by the body of the host. Yet, this consideration is valid only as long as the bird is alive. After the death of the bird their behaviour causes the accumulation on the head where they remain without any attempt to leave the dead host. At the head and especially around the bill the Ischnocera have a more exposed position than in the plumage of the body. Thus they will more easily come into contact with a new host. Owing to the host-specificity of the Mallophaga (Hopkins 1949, p. 421; Clay 1949, p. 282) their chances of a successful transfer must be very small but might be possible in the bird's nest or amongst gregarious birds especially in dense colonies. Nevertheless, in most cases these Mallophaga are destined to die after the death of their host. Thus, in most cases, the migration to the head seems to be of little importance as a means of transfer to a new host. All the same, the migration to the head may be explained as follows:

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after the death of the host the behaviour of the parasites on the single feather gets abnormally pronounced so that the animals pass by the quill of the feather and agglomerate on the bird's head. This reaction might then be regarded as irrational and without any importance to the continued existence of the species.

**e. Reaction to airstreams**

When exposed to a stream of air the specimens of *Columbicola columbae* immediately stop moving and press up to the vane. This reaction caused the accumulation close to the slit during the experiments with alternative temperatures (p. 177). If the airstream becomes more powerful the specimens force themselves down between the barbs so that only one lateral margin is visible in the vane. On a pigeon the specimens on the distal part of the remiges are mostly found in this position. Here they are exposed to airstreams every time the pigeon flies or flaps its wings. This reaction of the insects has also been released by fastening a remex to a rotating fan. On a feather left unmoved they stay on the surface of the vane and migrate to the base. On the proximal part of the remiges sheltered by the wing-coverts the Mallophaga are also found on the surface of the vane.

In the position between the barbs the specimens are evidently more protected against hard conditions during flight. There is no risk of their falling off since they stick very hard to the vane. It is more likely that they will be damaged by desiccation.

**VII. Discussion**

It has been stated in this paper that *Columbicola columbae* is not attracted by the temperature of its host. It has also been mentioned that only four experiments have previously been concerned with the thermal ecology of the Mallophaga (vide above p. 178—179). The first of these experiments deals with a kinetic reaction to high temperatures (Barber 1923) and no conclusions can be drawn about the reaction to the temperature of the host. In the second there is no statement as to which species was observed (Eichler 1936 b). The third apparently gave abnormal results (Bair 1950). The fourth demonstrates undoubtedly a positive response to the temperature of the host in some species (Conci 1952). As regards *Columbicola columbae* his result can hardly be correct. Our knowledge of the temperature reactions in the Mallophaga is thus very indefinite. Many authors have probably drawn conclusions from the reaction of Anoplura, which are very well investigated and known to "prefer" temperatures approximating that of the host (orientated by klinokinesis and klinotaxis) to the effect that in many surveys the Mallophaga are generally said to be positive to the body temperature of their host. Such a statement has no real foundation.

There are, however, so many observations indicating that certain Mallophaga really are positive to the warmth of the host (e.g. Lyonet 1829, p. 261; Eichler 1936 b, p. 480; Conci 1952) that this opinion cannot be disregarded. Thus the Mallophaga seem to differ in their temperature reactions and an attempt will now be made to discuss how this difference may be distributed. (The Rhynchophthirina differ so much from the rest of the...
Mallophaga, even biologically, Weber 1939, that they will be left out of the discussion.)

Only two species of the superfamily Amblycera living on mammals have been studied, viz. *Gyropus ovalis* Burm. and *Gliricola porcelli* Schrank, both living on *Cavia porcellus* L. The investigation made by Ewing (1924) gives many interesting results. According to him, both species, when resting, hold their heads against the skin of the host. *Gyropus ovalis* never walks backward and *Gliricola porcelli* never sideways (l.c. p. 3—5). Thus the species seem to have a specialized locomotion but no statement about their reaction to temperature can be based on that observation. Ewing remarks (p. 5): "The fact that the lice on the guinea pig remain so constantly next to or near the skin indicates again that the warmth of the body attracts them, yet we are not warranted in concluding that this is the fact without a demonstration under experimentally controlled conditions."

One investigation as regards the response to temperature has yet been made with the Amblycera living on birds. Conci (1952) has found that *Menopon gallinaceum* L. agglomerate at 39° C. and *Menacanthus cornutus* Schömmer at 42° C. His results that they are positive to the body temperature of the host agree very well with the conception about the biology of the Amblycera: they move quickly and are better suited to running than to climbing, they often migrate to the person who handles their dead host or try to leave it for a new one (Mjöberg 1910, p. 11; Eichler 1936 b, p. 473—480, 1952 b, p. 10; Blagoveshchenskii 1950, p. 110). Of course this transfer is facilitated if they are attracted by the temperature of the host.

Of the superfamily Ischnocera, no species living on mammals (Trichodectidae) have been ecologically investigated. It has been found that the number of *Damalinia bovis* L. (Crawford-Bensen 1941, p. 345) and *D. ovis* Schrank (Scott 1952, p. 66) decreases during the hot season. The authors do not mention if the specimens then preponderate in more sheltered places on the host, as is shown by Brinck (1948, p. 142).

Apart from the present paper, only three previous investigations deal with the Ischnocera living on birds as regards their temperature response. The experiment made by Barber (1923, p. 393) demonstrates a kinetic reaction to lethal high temperatures in *Bruléia vulgata* Kellogg. The result from Bair’s experiment (1950) with *Cuculogaster heterographus* Nitzsch has already been discussed, and I cannot regard it as representative of normal conditions. Besides his experiment with the Amblycera, Conci has investigated three species of Ischnocera, viz. *Cuculogaster heterographus*, *Columbicola colubrae*, and *Goniodes gigas* Tasch. His results show a positive reaction to a temperature of 35—37° C. in the three species. Concerning *Columbicola colubrae*, his result is quite contrary to my own. It is possible that his material has been too small.

The biology of the Ischnocera may give some guidance as to their reaction to temperature: they have a particular way of moving, they move slowly and after the death of their host they migrate to its head and remain there, making no attempts to reach a new host (cf. Eichler 1936 b. Blagoveshchenskii 1950). The coherence between the specialized way of moving and the migration to the bird’s head has already been stated (vide above p. 184). It is thus very probable that at least many Ischnocera behave in the same way as has been demonstrated in *Columbicola colubrae*, and are not susceptible to the temperature of their

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host. As long as the bird is alive, the Ischnocera as well as the Amblycerica migrate to the body of the host when they become irritated, although this reaction is due to quite different physiological activities. After the death of the host most Ischnocera accumulate on the bird's head, where they are well exposed and sometimes may come into contact with a new host. The Amblycera may be able to reach a new host by active searching as has been reported by Dubinin (1948, p. 206) about Colpocephalum sp. It is an interesting fact that, apart from cases of phoresy, all species of Mallophaga found separate from a host belong to the Amblycera (Thompson 1936, p. 95; Dubinin 1948, p. 208, Eichler 1952 a).

An ecological difference of the kind just described between the Ischnocera and the Amblycera living on birds would be a parallel to several bionomical differences between the groups, e.g. the feeding habits (Eichler 1937, Blagoveshchenskii 1949 and 1950, Crutchfield & Hixon 1943, Waterhouse 1953) and the position at copulation (Sikora & Eichler 1941). However, neither the Amblycera nor the Ischnocera seem to be quite uniform bionomically. Thus it is probable that the reaction to temperature differs within the two superfamilies or at least within the Ischnocera, which is the most heterogenous group. Therefore, this investigation will be extended in the future to a comparison between various species, in order to study the frequency of the specialized behaviour presented in this paper.

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HÅKAN STENRAM
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columbae L. (Mallophaga)

SÄRTRYCK UT "OPUSCULA ENTOMOLOGICA", BAND 21, 1956