LIFE HISTORY AND HABITS OF THE PIGEON LOUSE
(Columbicola columbae [Linnaeus])

Thesis

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Introduction

Very little work has been done on the life history or habits of Mallophaga. Only two papers have been published* which give even a general discussion of the life history of these parasites. The number of instars through which the insects pass was not determined in either case. For the experiments reported in this paper the pigeon louse (Cumbicola columbae [Linnaeus]) was chosen because of the ease of obtaining and handling the common host, Columba livia Linn.

Acknowledgements

Before proceeding further, the writer wishes to express her thanks to Dr. M.A. Stewart, under whose direction this work was done, for frequent suggestions and encouragement. Thanks are also due Dr. F.H. Wilson of Tulane University for a number of determined specimens of various species and for the use of his unpublished thesis on Mallophaga, as well as

* Notes on the Life History and Habits of Mallophaga - B.A. Barber, Fprs. Mich. Acad. Sci. 1921 pp. 391-395.
Some External Parasites of Poultry - G.W. Herrick, Cornell Univ. Coll. of Agri. Bul. 359, Apr. 1915.

for his many valuable suggestions. I also wish to thank Mr. H.C. Matthes of Rice Institute for the collection from time to time of the pigeon host.

Technique

Live specimens of Columbicola columbae were collected from freshly killed pigeons according to the method developed by F.H. Wilson (1928). The birds were wrapped in cotton and, since most external parasites leave the host when it becomes cold, the lice migrated to the cotton through which they could make little or no progress. Specimens were also collected from live birds, the birds being etherized and the feathers on which the lice were found clipped. By keeping pigeons in captivity, a constant supply of adults was assured.

The lice were kept in an incubator at 37°C. (+ or - .5° to 1°) which was found to be the most favorable temperature for this species. Temperatures ranging from 33°C. to 42°C. were tried. Oviposition occurred infrequently at the various temperatures and the resulting nymphs died within a few days after hatching. A water surface 12.5 inches square was exposed on the floor of the incubator to provide the necessary humidity. The lice were placed on feathers from the breast region of the bird and kept in open petri dishes. Several

unsuccessful attempts were made to rear the lice in capsules attached to the skin on the bird's back, one feather being enclosed in the capsule, but the bird always succeeded in loosening the capsule, thus allowing the lice to escape.

Specimens for microscopic study were preserved by being cleared in 10% KOH, completely dehydrated in a series of graduated alcohols, transferred to clove oil and mounted in Canada balsam. This method, however, could not be used to preserve the soft-bodied nymphs; for these it was necessary to reduce the clearing agent to a 5% solution and, besides the alcohols, momentary immersion in ether was used to complete the dehydration. The rest of the process was completed as above.

Synonymy

The original name of the species under discussion was Lipeurus columbae, described by Linnaeus in 1758. According to Harrison (1916017), a synonym was created by Nitzsch in 1866 when he described the species as Lipeurus baculus. In 1916, Harrison created the genus Esthiopterum for certain species of Lipeurus including L.columbae. The genus Esthiopterum was subdivided by Ewing in 1929 and the genus Columbicola was created, in which was included Esthiopterum columbae. The

valid name of the species is therefore Columbicola columbae (Linnaeus).

Host List

Columbicola columbae is common on both wild and domestic pigeons (Columba spp.). It has been reported from "nineteen of the forty pigeon host species". (Herrick, 1915). It has been reported from domestic pigeons all over the United States (and apparently is common in Europe); from the Canal Zone, Panama; from the province of Shinano, China; and from Calcutta, India. It has also been reported from the Chinese turtle dove, Streptopelia (Turtur) chinensis Ingram, and the Formosan green pigeon, Sphenocercus formosae, both of Formosa.

It was reported from the Common Noddy, Anous stolidus Linn., of the Galapagos Islands; from Geospiza fuliginosa Gould and Camarhynchus pallidus Sclater and Salvin (C. productus), both Galapagos finches; and from Nesomimus melanotis Gould, the Galapagos Mockingbird. Considerable interest may be attached to these latter reports, which were made by Kellogg and Kuwana (1902), due to the fact that Mallophaga are coming into use as a means of determining the phylogenetic relationships of birds.

Hippoboscids Carriers of Mallophaga

Eleven authentic records of Hippoboscids being found with Mallophaga on them have been recorded through 1927. Most of

these records are for Ornithomyia avicularia Linnaeus. Six of the Mallophaga reported were of the genus Degeeriella, one of the genus Philopterus, and the others were not determined.

While collecting lice from pigeons, the writer also collected at different times four Hippoboscid flies which were determined as Pseudolynchia maura Bigot. One of the flies was carrying three specimens of Columbicola columbae, two females and one male. Another fly was carrying one male. It may be seen from this that, since the fly is not confined to one bird during its entire life, Pseudolynchia may be, and probably is, an important agent in the dispersal of C. columbae.

Feeding Habits

The feeding habits of Mallophaga have not been studied to any great extent. It is generally conceded in textbooks of entomology that they feed on feathers, scales of skin and dried blood. Waterston (1926) writes, "Nothing seems to come amiss to the Mallophaga as food. The protecting sheaths of growing feathers, feather fibre, down, skin, scurf, scabs, blood (when available), etc. are all eaten; they devour, too, their own egg shells, and cast off skins and perhaps occasionally indulge in cannibalism, for I have recently examined a crop of the large G. bicuspidatus which was crammed solely with fragments of Goniocotes diplogonus, some of which appeared not to be of exuvial origin."

I have never observed Columbicola columbae to feed on

anything other than the barbules of the feathers, except in one case. A nymph in the first instar was placed on a white feather with a drop of blood smeared on the fluffy part. On the following day the alimentary tract of the nymph was a dull red, the insect evidently having fed on the blood. This specimen died two days later. Six other nymphs were placed on a fresh feather with blood but none of them fed on the blood over a period of seven days. Two nymphs placed on a blood clot in a petri dish died the following day without having fed.

A male was placed on a fresh epidermal scale taken from a pigeon. This specimen failed to feed during an hour but, when placed on a feather, fed at irregular intervals over a period of twenty minutes. Two newly hatched nymphs placed on epidermal scales died without having fed.

Adults and nymphs in all stages of development may be observed feeding frequently on the barbules, nearly always those near the proximal end of the feather. There seems to be a decided preference for the feathers from the breast region of the bird when the lice are raised in an incubator, though they are rarely found in that region of the bird. Where both types of feathers were available in the dish, the lice migrated to the fluffier feathers, only occasionally returning to the flight feathers. The adults are commonly

found on the long flight feathers of the bird's wing; the nymphs (and occasional adults, most of which are females) are found on the feathers at the back of the head.

Copulation

Mating occurs frequently and may be observed at almost any time. The process is easily seen with a binocular microscope. The male may be observed to approach a quiescent female and clasp her abdomen at the third or fourth segment with his antennae. After a few moments, he moves up, taking his position beneath the female, clasping her ptero-thorax just in front of the coxae of the third pair of legs and curving the end of his abdomen up to meet hers. Coition is interrupted every two to three minutes at which times the male would retreat a little, again clasping the third or fourth abdominal segments of the female with his antennae. If the pair were touched by other individuals, the procedure was almost invariably repeated. The female usually defaecates at the end of fifteen to twenty minutes, the male at twenty-five to thirty minutes. There are periods of several seconds of rest during which the male remains with his antennae clasping the pterothorax of the female. Coition lasts for varying lengths of time, the shortest observed time being about ten minutes and the longest being one

hour and fifteen minutes. Frequently, a male may be observed to approach a quiescent female and clasp her abdomen with his antennae; then, though she makes no move to escape, he may release her and move on.

While mating, the female rarely moves unless it is to free herself from the male. In doing this, she runs rapidly in and out among the fluffy barbs near the proximal end of the feather. The male, while still clasping the female around either the pterothorax or abdomen with his antennae, is at a disadvantage and is usually dislodged within thirty seconds to two minutes.

Oviposition

Oviposition occurs even when the lice are removed for observation from the incubator to the somewhat cooler atmosphere of the room. The egg is plainly visible within the female's abdomen about forty-five minutes before oviposition occurs. It extends from the third to the fifth abdominal segments. As oviposition begins, the female grasps the feather firmly with her mandibles and legs. The tip of the abdomen is raised to about a 45° angle but is lowered as soon as the egg begins to appear. The egg is extruded until all but the tip is exposed. The female then releases her hold on the feather and moves actively about until the egg is released.

In the incubator, the eggs are usually found in the dish. If they are attached to the glass, they are usually erected at a 40° to 50° angle. In at least 50% of the cases, the eggs were not cemented to anything but were lying loose in the dish. In only a very few instances were the eggs glued to a feather in the incubator. The female shows little preference in placing the eggs when ovipositing on feathers in the incubator. Eggs collected from the pigeon, however, show a definite arrangement. They are always found on the feathers on the underside of the wing, principally on the long flight feathers though some may be found on the lesser wing coverts. The eggs lie on the side of the feather next to the bird's body in the deep grooves formed by the barbs, the proximal end being glued against the shaft. The operculum is pointed toward the edge of the feather. Numerous eggs are laid on the same feather, there being from ten to twenty eggs on the feathers of birds with average infestations. As many as sixty eggs have been found on a single feather.

Over a period of five days, seventeen females laid forty-four eggs, averaging .52 eggs per day per female. In another count, six females laid twelve eggs over a period of six day, averaging .33 eggs per day per female. Nine females laid seventeen eggs during six days, averaging .31 eggs per day per female.

Hatching

The process of hatching in Columbicola columbae is easily observed under the medium power objective of a compound microscope. The nymph, when ready to emerge, begins pumping in air through the mouth. The air bubbles accumulate in the digestive tract until pressure forces them into the egg shell at the posterior end. After about five minutes, the pressure behind the nymph is sufficient to cause the operculum to burst open. The air pumping is slowed somewhat for six to eight minutes until the second pair of legs is nearly freed. It increases in rapidity for a minute or two and then slows again. The freeing of the rest of the body is aided by muscular contraction and expansion of the abdomen. The head, which in the embryo is folded against the ventral aspect of the thorax, is erected twelve to fifteen minutes after the cap is burst, at about the same time that the second pair of legs is freed. The third pair of legs is freed two to three minutes later. Within another five minutes, the caudal hairs are freed and the egg-shell is left. Immediately upon hatching, the nymph readily grasps a feather and moves actively about. Feeding does not take place, however, until several hours later.

Metamorphosis

There are three instars in the developmental cycle of

Columbicola columbae and three molts occur before the insect reaches the adult stage. [For the length of time elapsing between the molts, see Table I]. In the course of these experiments, only three of the specimens collected soon after hatching were reared to maturity. Two of the specimens were females and one was a male. The length of the egg stage for these lice is not known, the eggs from which they developed having been collected from the bird.

Data for the second and third instars as recorded in Table I were obtained almost entirely from nymphs in various stages of development collected from the host and reared in the incubator.

The egg (Fig. 1) is white and, when first laid, is opaque. Later, the embryo can be plainly seen within (Fig. 2). When the egg is laid, it is cemented at the proximal end, the distal end being free and erected. Frequently, as mentioned above, the egg cement hardened before it came into contact with anything. The egg shell is fairly resistant and can withstand considerable pressure.

When first hatched, the young nymph (Fig. 3) is white, the only chitinized area being the mandibles. By the time the nymph is a day old, the clypeal band is a pale yellow, due to slight chitinization. Segmentation of the abdomen is very indistinct.

The insect at this stage in its development is very active. It feeds frequently and the ingested material can be plainly seen, through the pale cuticula, lying in the crop. The flattened spine on the clypeal margin, which is an important distinguishing character of the genus, is not present in the first instar. A dark eye spot is present immediately posterior to the first antennal segment.

In the second instar (Fig. 4), the flattened spine is present on the clypeus. The head is well-chitinized, as are the antennae and the pleurites of both the thorax and abdomen.

In the third instar (Fig. 5), the head, antennae, thorax and abdominal pleurites are well-chitinized, as are the tarsi and claws. After the third molt, the insect reaches the adult stage and the eye-spot is no longer present. The process of molting was not observed for any of the instars.

The adult (Fig. 6) is heavily chitinized except for a narrow, mid-dorsal line on the abdomen. The antennae are different in the two sexes. The male has a short appendage on the third antennal segment, the antennae being adapted for clasping the female while mating.

Measurements for the various stages will be found in Table II. In order to increase as much as possible the

accuracy of all data, the Gaussian formula for calculating the probable error was used. The formula is as follows:

$P.E. = \pm .6745 \times \frac{\sigma}{\sqrt{n}}$ where σ is the standard deviation and n is the number of samples used. Where less than sixteen samples are used, the Bessel formula is more nearly correct (Wardle, 1929):

$$P.E. = \pm \frac{.6745 \times \sigma}{\sqrt{n - 1}} .$$

Conclusion

The life cycle of Columbicola columbae may be summarized as follows: The egg stage usually lasts 4.15 days with a probable error of $\pm .103$ days. The average length of the first instar is 6.73 days, with a probable error of $\pm .076$ days. The second instar average was 6.72 days with a probable error of $\pm .064$ days. The third instar averaged 6.77 days with a probable error of $\pm .025$ days. These averages are fairly accurate as may be seen by comparison with the data of the three life cycles which were completed. In these completed cycles, the first instar was seven days for all three specimens. The second instar for the females was six and eight days, and for the male six days. The third instar for the two females was seven and eight days, and for the male six days.

The metamorphosis of C. columbae is greatly slowed by a reduction of 4°C. in temperature. This was demonstrated by the fact that, whereas the egg stage at 37°C. was normally

from three to five days, at 33°C., it ran from nine to fourteen days. At the latter temperature, the nymphs nearly always died in from one to six days, though the adults lived as long as twenty-nine days. Two females lived fifty-one days at 37°C., the usual time being from thirty to forty days. Temperature is probably, therefore, the chief factor in determining not only the length of the life cycle but also the percentage of survival of the young.

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Table I

Stages in the Development of Columbicolacolumbae Linn.

Egg Stage

Oviposited	Hatched	
12-26-32.....	12-29-32.....	3 days
1--6-33.....	1-12-33.....	6 "
1--5-33.....	1-13-33.....	8 "
1--6-33.....	1-13-33.....	7 "
2-17-33.....	2-22-33.....	5 "
2-22-33.....	2-27-33.....	5 "
2-23-33.....	2-27-33.....	4 "
2-24-33.....	2-27-33.....	3 "
2-24-33.....	2-28-33.....	4 "
4-10-33.....	4-15-33.....	5 "
4-10-33.....	4-15-33.....	5 "
4-10-33.....	4-15-33.....	5 "
4-10-33.....	4-15-33.....	5 "
4-10-33.....	4-15-33.....	5 "
4-12-33.....	4-15-33.....	3 "
4-14-33.....	4-17-33.....	3 "
4-14-33.....	4-17-33.....	3 "
4-14-33.....	4-17-33.....	3 "
4-14-33.....	4-17-33.....	3 "
4-14-33.....	4-17-33.....	3 "
4-14-33.....	4-17-33.....	3 "
4-14-33.....	4-17-33.....	3 "
4-14-33.....	4-17-33.....	3 "
4-14-33.....	4-17-33.....	3 "
4-14-33.....	4-17-33.....	3 "
4-28-33.....	5--3-33.....	5 "
		26 <u>108.00</u>
		4.15 average
Standard deviation: $\pm$.78		
Probable error.....: $\pm$.103		

First Instar

Hatched	First Molt	
12-3-32.....	12-16-32.....	8 days
12-15-32.....	12-23-32.....	8 "
2-21-33.....	2-28-33.....	7 "
2-27-33.....	3--9-33.....	10 "

3-14-33.....	3-18-33.....	4	days
3-14-33.....	3-19-33.....	5	"
3-16-33.....	3-20-33.....	4	"
3-16-33.....	3-20-33.....	4	"
3-17-33.....	3-22-33.....	5	"
3-16-33.....	3-23-33.....	7	"
3-16-33.....	3-23-33.....	7	"
3-22-33.....	3-29-33.....	7	"
3-29-33.....	4--6-33.....	8	"
4--7-33.....	4-14-33.....	7	"
4--7-33.....	4-14-33.....	7	"
4--8-33.....	4-14-33.....	6	"
4-17-33.....	4-24-33.....	7	"
4-17-33.....	4-24-33.....	7	"
4-17-33.....	4-24-33.....	7	"
4-17-33.....	4-24-33.....	7	"
4-17-33.....	4-24-33.....	7	"
4-17-33.....	4-24-33.....	7	"
4-17-33.....	4-24-33.....	7	"
4-17-33.....	4-24-33.....	7	"
4-17-33.....	4-25-33.....	8	"
4-18-33.....	4-25-33.....	7	"
		26	<u>175.00</u>
			6.73 average

Standard deviation: $\pm .58$
 Probable error.....: $\pm .076$

Second Instar

First Molt

Second Molt

2-28-33.....	3--6-33.....	6	days
3--4-33.....	3-10-33.....	6	"
3--6-33.....	3-13-33.....	7	"
3-23-33.....	3-29-33.....	6	"
3-28-33.....	4--3-33.....	6	"
3-28-33.....	4--3-33.....	6	"
3-28-33.....	4--3-33.....	6	"
3-29-33.....	4--6-33.....	8	"
4--6-33.....	4-13-33.....	7	"
4--8-33.....	4-15-33.....	7	"
4--8-33.....	4-16-33.....	8	"
4-10-33.....	4-17-33.....	7	"
4-10-33.....	4-17-33.....	7	"
4-14-33.....	4-22-33.....	8	"
4-22-33.....	4-26-33.....	4	"

4-24-33.....	5--1-33.....	7 days
4-24-33.....	5--1-33.....	7 "
4-25-33.....	5--1-33.....	8 "
		18 <u>121.00</u>
		6.72 average

Standard deviation: $\pm .4$
 Probable error.....: $\pm .064$

Third Instar

Second Molt

Third Molt

1-13-33.....	1-19-33.....	6 days
2-23-33.....	3--3-33.....	8 "
2-23-33.....	3--3-33.....	8 "
2-23-33.....	3--3-33.....	8 "
2-28-33.....	3--5-33.....	6 "
3--6-33.....	3-13-33.....	7 "
3-23-33.....	3-28-33.....	5 "
3-29-33.....	4--4-33.....	6 "
4--4-33.....	4-10-33.....	6 "
4--6-33.....	4-14-33.....	7 "
4-17-33.....	4-24-33.....	7 "
4-22-33.....	4-30-33.....	8 "
4-26-33.....	5--1-33.....	5 "
		13 <u>88.00</u>
		6.77 average

Standard deviation: $\pm .13$
 Probable error.....: $\pm .025$

Life cycle from hatching to adult

First Instar

2-21-33.....	2-28-33.....	7 days
3-16-33.....	3-23-33.....	7 "
3-22-33.....	3-29-33.....	7 "

Second Instar

2-28-33.....	3--6-33.....	6 days
3-23-33.....	3-29-33.....	6 "
3-29-33.....	4--6-33.....	8 "

Third Instar

3--6-33.....	3-23-33.....	7 days
3-29-33.....	4--4-33.....	6 "
4--6-33.....	4-14-33.....	8 "

Table II - Measurements

Egg

Length	Width
.720.....	.210
.703.....	.204
.720.....	.186
.714.....	.198
.696.....	.204
.684.....	.210
.703.....	.204
.660.....	.204
.714.....	.192
.696.....	.198
av. .702 mm.	av. .201 mm.

Standard deviation: $\pm .016$ $\pm .0707$
 Probable error.....: $\pm .003$ $\pm .015$

First Instar

Head	Thorax	Abdomen	Total
.270	.186	.348	.804
.276	.180	.396	.852
.258	.204	.408	.870
.276	.180	.348	.804
.270	.186	.408	.864
.216	.180	.378	.774
.270	.180	.354	.804
.264	.174	.360	.798
.288	.174	.372	.834
.300	.180	.366	.846
.270	.174	.378	.822
		av. .824 mm.	

Standard deviation: $\pm .008$
 Probable error.....: $\pm .001$

Second Instar

Head	Thorax	Abdomen	Total
.336	.228	.690	1.254
.324	.210	.618	1.152
.354	.228	.564	1.146
.348	.216	.696	1.360
.342	.234	.672	1.248
.336	.210	.660	1.206
		av. 1.227 mm.	

Standard deviation: $\pm .04$
 Probable error.....: $\pm .012$

Third Instar

Head	Thorax	Abdomen	Total
.450	.306	.912	1.668
.432	.330	.870	1.632
.438	.318	.960	1.714
.420	.258	.840	1.518
			av. 1.633 mm.

Standard deviation: $\pm$.421

Probable error.....: $\pm$.166

Male

Head	Thorax	Abdomen	Total
.522	.426	1.266	2.214
.522	.426	1.308	2.256
.534	.469	1.404	2.406
.510	.426	1.302	2.238
.534	.426	1.620	2.580
.504	.426	1.260	2.190
.522	.450	1.596	2.568
.546	.450	1.266	2.262
.450	.414	1.194	2.058
.504	.426	1.260	2.190
.504	.438	1.272	2.214
			av. 2.289 mm.

Standard deviation: $\pm$.109

Probable error.....: $\pm$.023

Female

Head	Thorax	Abdomen	Total
.522	.456	1.806	2.314
.552	.426	1.650	2.628
.534	.390	1.578	2.502
.522	.426	1.692	2.640
.560	.408	1.632	2.600
.528	.414	1.638	2.580
.522	.450	1.710	2.682
.594	.450	1.800	2.844
.564	.414	1.686	2.664
.558	.426	1.650	2.634
.558	.462	1.764	2.814
.558	.432	1.686	2.676
			av. 2.673 mm.

Standard deviation: $\pm$.09

Probable error.....: $\pm$.018

Explanation of Figures

- Fig. 1 - The egg of C. columbae
- Fig. 2 - Egg showing nymph in position, shortly before hatching
- Fig. 3 - Nymph just emerged from egg
- Fig. 4 - Nymph just after first molt
- Fig. 5 - Nymph just after second molt
- Fig. 6 - Adult female; also antenna and posterior abdominal segments of male

Stippling indicates parts darkened by chitinization

All figures drawn to scale except Fig. 6 which is drawn to half scale.

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6