THE DISTRIBUTION OF MALLOPHAGA ON THE DOMESTIC PIGEON (COLUMBA LIVIA)

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(Received 25 June 1970)

Abstract

NELSON B. C. and MURRAY M. D., 1971. The distributions of Mallophaga on the domestic pigeon (Columba livia). International Journal for Parasitology, 1: 21–29. The distribution of Hohorstiella lata, Colpocephalum turbinatum, Campanulotes bidentatus compar, and Columbicola columbae on domestic pigeons were determined. Each species laid its eggs on a different part of the body but all fed on the fluffy part of the body feathers. H. lata also fed on blood, and C. turbinatum on its own eggs and nymphs. Reduction of the efficiency of preening led to an increase in the number of lice and more widespread distribution of nymphs and adults but not to a rapid change in the distribution of eggs. It is suggested that preening has played a major selective role, and that the morphological and behavioural adaptations of the lice are to ensure that they and their eggs survive this type of predation.

INDEX KEY WORDS: Avian lice; Mallophaga; Campanulotes; Columbicola; Colpocephalum; Hohorstiella; domestic pigeon; Columba livia; distribution on host; effect of preening.

INTRODUCTION

ALTHOUGH much has been written on the taxonomy and evolution of avian Mallophaga there are few detailed studies of their biology apart from the recent work of Kalamarz (1963) on the lice of domestic fowl (Gallus gallus), of Baum (1968) on the lice of the blackbird, Turdus m. merula (L.), and those mentioned by Blagoveshchenskii (1959).

A study of the lice of the domestic pigeon, *Columba livia*, was undertaken because two of the four species found on pigeons in Australia are amblyceran and two are ischnoceran. One representative of each of these groups is stated as being associated with the body and one with the wing. It was found in fact that they have many ecological similarities, and that the convenient division into body and wing lice is biologically misleading.

MATERIALS AND METHODS

The pigeons used in the studies were feral domestic pigeons, *Columba livia* (Tumbler strain) of both sexes and of unknown age. Their colours varied from light to dark grey and included some which were brown barred. They were fed on grain and kept in windowed rooms, the temperature of which varied from 10 to 23°C.

Lice were killed quickly in situ so that their distribution could be determined. Paper towelling was first placed under the wings to prevent movement of lice to and from the body, and then wrapped around the body. A large wad of cotton wool soaked with ether or chloroform was immediately placed around the body, and the neck of the pigeon was broken or the bird was killed with ether or chloroform. The dead bird, enveloped in towelling and cotton wool, was placed in a plastic bag and kept deep frozen until examined. All birds were thawed for examination, and injected with 40% formalin to preserve the carcase and to facilitate the removal of feathers.

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The body of the pigeon was classified into nine regions. The head was further subdivided into the crown, gular and nape regions; the neck extended from the head to the anterior of the sternum; the breast region covered the sternum; the vent extended from the posterior of the sternum to the undercoverts of the tail; the sides were the parts covered by the secondary feathers of the folded wing; the back extended from the anterior of the wing attachment to the oil gland and thus included part of the rump; the tail extended posteriorly from the oil gland. The two remaining regions were the wings and the legs.

Feathers were plucked from a region or removed individually. All feathers were examined individually under a stereo-microscope to determine the distribution and number of each stage, and whether the eggs were dead, living or hatched. The description of the parts of an individual feather (Fig. 3) follows that of Voitkevich (1966), and the nomenclature of Van Tyne & Berger (1959) has been used for the general feather types and their detailed structure.

Attempts were made to rear each species of louse in small glass jars or cells. The cells in which lice were placed, and the methods used to control temperature, relative humidity and temperature gradients have been described previously (Murray, 1957, 1960). The presence of blood in the crop was detected with the benzidine test, and feather particles by dissection and examination of the contents of the crop under a compound microscope.

Species of lice

Four species of lice were studied, and the nomenclature used follows that of Emerson (1957). The ischnoceran species were Campanulotes bidentatus compar (Burmeister, 1838) and Columbicola columbae (Linnaeus, 1758). The amblyceran species were Hohorstiella lata (Piaget, 1880) and Colpocephalum turbinatum Denny, 1842. There was no difficulty in differentiating the eggs of these species by size and shape. The nymphs of H. lata were identified by the setal pattern of the gular plate, and those of C. b. compar and C. turbinatum by size (Nelson, unpublished data). Martin (1934) has described the differences between the nymphal instars of C. columbae.

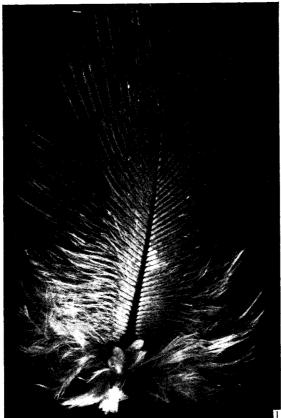
The distribution of lice

The distribution of the four species of lice was determined in detail on three pigeons for each species by examining every feather. The results are shown in Tables 1 and 2. The number of eggs are total counts and include living, dead and hatched eggs. The subsequent examination of 20 living or dead pigeons confirmed these findings.

Campanulotes bidentatus compar (Table 1). Eggs were found on the neck, back, sides, breast, vent and wings, very few were found on the head and legs, and none on the tail. On the wings they were attached to the overcoverts adjacent to the back. One to two were laid in the silky part of the body feathers with the end of attachment towards the skin. Nymphs and adults were found mostly on the neck, back, sides, breast and vent, usually in the ventral fluffy part of the feather near to the rachis.

Hohorstiella lata (Table 1). Eggs were restricted to the head particularly the gular area. The large eggs were easily seen, and 1–10 eggs were attached to the ventral surface of the feather with the end of attachment towards the skin (Fig. 1). In heavy infestations eggs were laid on top of one another (Fig. 6). Nymphs and adults were found scattered over the body, and moved rapidly over the surface of the skin.

Columbicola columbae (Table 2). Eggs were found mostly on the wings but some were on the head and a few on the neck, sides and breast. On the wings they were laid mostly on the ventral surface of the first rows of undercoverts. Eggs were laid in the furrows between



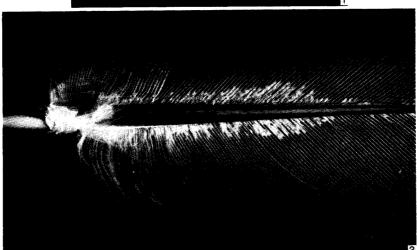


FIG. 1. Eggs of *H. lata* laid on feather from head of pigeon. Several eggs may be laid on each feather, alternately on each side of the rachis with the end of attachment towards the skin.

Fig. 2. Eggs of *C. turbinatum* laid on the ventral surface of a primary feather of the wing of pigeon. Several eggs may be laid near to the rachis in each furrow between the barbs. Most of the eggs in the photograph have hatched. (Photographs by I. Roper).

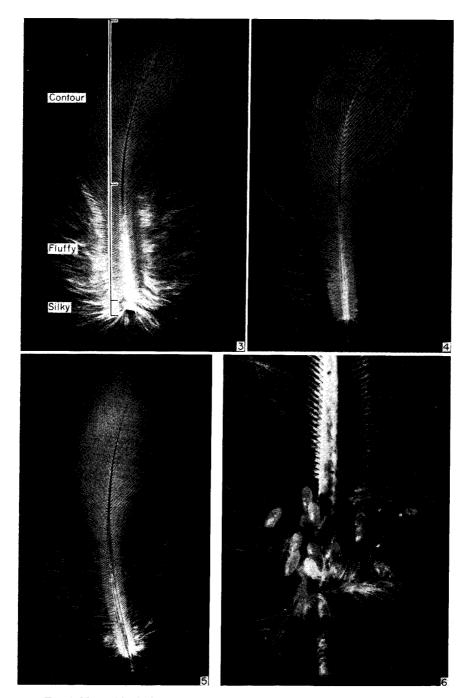


Fig. 3. Normal body feather of pigeon showing contour, fluffy, and silky part.

Fig. 4. Body feather showing fluffy part eaten by C. columbae.

Fig. 5. Body feather showing fluffy part eaten by C. turbinatum.

FIG. 6. Large egg mass of *H. lata*. Much of the fluffy part of the body feather has been eaten. (Photographs by I. Roper; Fig. 6 from C.S.I.R.O., *The Insects of Australia*, Melbourne University Press, 1970, by permission.)

Table 1—Number and distribution of lice (Campanulotes b. compar and Hohorstiella lata) on body of domestic pigeon (Columbia livia)

Species of louse	Identity of pigeon	Instar	Region of body									Total num- ber of
			Head	Neck	Back	Sides*	Breast	Vent	Tail	Legs*	Wings*	each instar
Campanu- lotes	Q	egg nymph	7	178	110	92	169	37	0	0		593
bidentatus		1	0	34	16	7	78	27	0	3	0	165
compar		2	0	17	14	17	63	32	1	6	0	150
		3	0	14	15	18	54	38	1	6	4	150
		male	1	12	31	42	21	33	3	1	6	150
		female	0	3	36	32	11	12	8	3	9	114
	A	egg nymph	0	33	120	72	49	100	0	6	281	661
		1	0	5	13	9	48	6	1	2	2	86
		$\overline{2}$	0	2	13	8	40	4	0	1	3	71
		3	0	2	12	6	35	6	0	. 0	2	63
		male	0	2	23	22	7	40	1	0	0	95
		female	0	1	20	12	8	44	1	0	1	87
	E	egg nymph	0	89	146	213	116	33	0	15	543	1155
		1	0	11	18	14	58	8	0	0	4	113
		2	0	8	30	13	68	9	0	1	3	132
		3	0	10	32	15	22	12	0	0	3	94
		male	2	21	25	24	6	54	0	0	3	135
		female	0	5	12	16	8	43	0	0	4	88
Hohor- stiella	Q	egg nymph	87	5	0	0	0	0	0	0	0	92
lata†		1	0	0	0	0	0	0	0	0	0	(
		2	0	0	0	0	1	0	0	0	0	1
		3	0	0	0	0	2	0	0	0	0	2
		male female	0 0	0 0	0 0	0 0	1 0	1 1	0 1	0 0	0 2	2
	1153	egg nymph	4049	0	0	0	0	‡11	0	0	0	4060
		1	0	8	6	15	5	10	0	0	0	44
		2	1	10	5	20	8	9	0	0	0	53
		3	0	5	6	8	4	24	0	1	0	48
		male	2	6	6	15	4	10	0	0	0	43
		female	10	10	24	24	14	15	3	2	2	104

^{*} Total of two sides, legs, or wings.

the barbs with the end of attachment towards the rachis. More than one egg was found in a furrow. Nymphs and adults were found particularly on the wings and the head, neck, back, sides and breast which are the anterior regions of the body.

Colpocephalum turbinatum (Table 2). Eggs were found principally on the wings but some

[†] The data from the third pigeon are not included because there were few eggs and lice.

[‡] All eggs were found on one feather.

Table 2—Number and distribution of lice (Columbicola columbae and Colpocephalum turbinatum) on body of domestic pigeon (Columbia livia)

Species of louse	Identity of pigeon		Region of body									Total num- ber
		Instar										of each
			Head	Neck	Back	Sides*	Breast	Vent	Tail	Legs*	Wings*	insta
Columbi- cola	A	egg nymph	28	7	0	9	0	0	0	0	4901	4945
columbae		1	4	27	12	10	6	2	0	1	20	82
		2	13	12	10	6	3	1	1	0	46	92
		3	13	11	8	7 9	4	1 2	1 4	1 0	47 80	93
		male female	0 1	5 0	17 20	16	1 2	8	11	0	68	118 126
	———- Е	egg	21	5	0	8	0	0	0	0	1306	1340
		nymph										
		1	3	15	24	12	5	0	0	0	32	91
		2 3	2	19	17	7 2	5 2	2 2	0	0	37 18	89 35
		male	1 0	7 1	3 4	2	0	2	0 4	0	37	50
		female	0	1	5	1	0	2	9	0	28	46
	Q	egg nymph	141	27	0	9	6	0	0	0	1302	1485
		1	14	21	3	6	4	1	0	2	2	53
		2	15	11	3	1	7	0	2	2	7	48
		3	2	7	3	0	1	0	1	1	18	33
		male female	0 2	1 2	1 1	4 2	2 1	0 1	4 10	0 3	17 19	29 41
Colpoce- phalum	1153	egg nymph	0	0	4	0	0	0	0	0	3898	3902
turbinatum		1	0	0	2	0	0	0	32	0	78	112
		2	0	0	5	0	0	0	71	0	7	83
		3	0	0	2	0	0	1	56	0	17	76
		male female	0 0	0 0	1 3	0 2	1 0	2 1	43 52	0 0	56 44	103 102
	1180	egg nymph	0	0	0	2	0	0	51	0	14,659	14,712
		1	0	0	2	2	0	11	28	0	565	608
		2	0	0	2	0	2	26	107	0	405	542
		3	0	0	2	0	0	20	97	1	270	390
		male	0	1	1	0	0	44	234	0	398	678
		temale	1	0		0	1	24	196	0	330	554
	1181	egg nymph	0	0	0	1	0	0	6	0	5849	5856
		1	0	0	1	0	1	1	2	0	214	219
		2	0	0	1	0	0	0	16	0	171	188
		3 male	0	0 0	1 2	2 0	0 1	0 0	28 46	1 1	127 113	159 163
		female	Ö	0	1	0	0	3	29	1	80	114

^{*} Total of two sides, legs or wings.

were found on the tail. They were laid on the ventral surface of the primaries, their over-coverts, and alulae with some on the first five secondaries. The small eggs were laid in the furrows between the barbs next to the rachis, and several eggs were found in a furrow (Fig. 2). The eggs were attached laterally with the operculum distal to the rachis. Nymphs and adults were mostly on the wings and tail where many were within the calamus, as noted by Selim *et al.* (1968), having entered through the upper umbilicus or a split which had developed distal to and continuous with the upper umbilicus. They were also found on the posterior parts of the body, vent and rump regions.

Effect of reduction of efficiency of preening

Ten pigeons known to be infested with $C.\ b.\ compar,\ H.\ lata$ and $C.\ columbae$ were divided into two equal groups. The upper bills of one group were clipped with sharp scissors to remove about 1 cm of the tip, the birds were kept in separate cages in the same room, and one normal and all those with clipped bills were weighed biweekly over a period of 3-6 months. The operation was repeated if the bill regrew too rapidly. The body weights of all but one of the pigeons remained fairly constant, fluctuating within ± 7 per cent of their original body weight. The lice on these birds were killed in situ and their distribution determined.

The upper bills of another 12 pigeons were clipped, and, in addition to confirming the previous findings, the effect on populations of *C. turbinatum* was determined and the change in the distribution of eggs of *H. lata* observed.

The influence on the numbers of lice

The number of lice on all birds with clipped beaks increased. However their numbers were obviously so much greater that no detailed counts were made. It was estimated that 20,000 eggs and 1–2000 nymphal and adult *H. lata* were on one bird before it lost weight—rapidly over two weeks—and died.

The influence on distribution of lice

Campanulotes bidentatus compar. Eggs, nymphs and adults increased in numbers on the neck, back, sides, breast, vent and wings, and 4–6 eggs were laid on a feather. However eggs were not found on the primary, secondary or undercovert feathers of the wings.

Hohorstiella lata. As the numbers of adults increased so did the number of eggs on the gular area of the head. Eggs spread over the head; and then down the neck. Eventually as the population exploded eggs were found on the breast, sides and vent, and 30–50 were laid on most feathers (Fig. 6). Nymphs and adults were abundant over the head, neck, sides, breast and vent.

Columbicola columbae. The number of eggs, nymphs, and adults increased on the wings and body, and as many as 300 eggs were found on single feathers on the wings. On the body feathers the eggs were attached to the rachis in the silky zone with their end of attachment towards the skin.

Colpocephalum turbinatum. The number of eggs increased only on the wings and tail, and more than 1000 eggs were found on one primary feather. Nymphs and adults however increased not only on the wings and tail, but also in the vent region.

Biology of the lice

Selected aspects of the oviposition and feeding behaviour of the lice were studied to determine their possible influence on the distribution of the lice on pigeons.

Campanulotes bidentatus compar. Attempts to establish colonies of this louse at 32°, 35° and 37°C at 75% r.h. failed. Body feathers were supplied for food, and adults survived 3 weeks.

Groups of 10 females were exposed to 31, 35 and 40°C at 75% r.h. with body feathers for 7 days. At 31 and 35°C, 8 females survived and 9 and 16 eggs were laid respectively. All the females exposed to 40°C died within 4 days, and 20 eggs were laid.

A group of females were placed in a cell together with body feathers and exposed to 35°C at 75% r.h. Eggs were laid on the silky, fluffy and contour parts of the feathers, 33 on the former two and 72 on the latter. The silky part of body feathers was removed and the remaining fluffy and contour part of four body feathers aligned longitudinally in a cell along which a temperature gradient from 17 to 41°C was established. A group of females was placed in the cell and examined 19 h later when 36 eggs had been laid, all within the 39–41°C zone. The gradient within the cell was reversed, and when re-examined 27 h later another 25 eggs had been laid at the opposite end of the cell, again in the 39–41°C zone.

Eggs, which were newly laid at 35°C and 75% r.h., were exposed to constant temperatures at 75% r.h. At 30°C none of 12 eggs hatched, at 35°C eight of 13 hatched, and at 40°C seven of 9 eggs hatched.

Hohorstiella lata. Attempts to establish colonies in the laboratory were not successful, and adults only survived 2 days at 37°C at 75% r.h. Feather particles and blood were identified in the crop. This louse feeds on the fluffy area of body feathers (Fig. 6) and blood was regularly seen in the crop. No eggs were laid in the laboratory experiments.

A pigeon with a heavy infestation was killed. Feathers with eggs were removed, and exposed to 30, 35, 37, 40 and 42°C at 75% r.h. Eggs hatched up to 10 days after exposure but, because they were of unknown age, only the data from those which hatched after 3 days are considered. At 30°C 4 out of 15 eggs, hatched at 35°C 17 out of 20, at 37°C 16 out of 17, at 40°C 13 out of 17, and at 42° 6 out of 16.

Columbicola columbae. Colonies of C. columbae were kept in the laboratory at 35°C and 54% and 75% r.h. for 2-3 months. Body feathers were supplied for food and renewed weekly.

C. columbae died when given only undercoverts on which to feed. Body feathers were essential and it was found that these lice fed on the fluff (Fig. 4). At 40°C no eggs were laid, and the lice died after 2 weeks.

Some of the colonies were examined daily to remove the newly-laid eggs which were exposed to 22, 25, 27, 31, 35, 38, 41 or 43°C at a r.h. of 33, 45, 75, 92, or 100%. It was not possible to collect all the eggs necessary at one time, so with every collection some were placed at 35°C and 54% r.h. as controls. A total of 13–20 eggs were exposed to 22 and 25°C, and 30–50 eggs at 27–43°C. As all control groups were similar the results are summarised in Fig. 7. It may be seen that most eggs developed and hatched between 31–38°C at 33–92% r.h. Some hatched at 27 and 41°C but all died at 22, 25 and 43°C.

Three groups of 5 males and 5 females were placed in glass tubes with contour and undercovert feathers and exposed to 54% r.h. at 25, 30, 35, 40 and 44°C at 54% r.h. The number of eggs laid and dead lice was recorded daily for 7 days. At 25°C, 3, 2 and 3 eggs were laid, 1 female was dead after 2 days and the remaining 14 females lived for 7 days; at 30°C, 15, 8 and 5 eggs were laid and 2 males were dead after 4 days; at 35°C 11, 8 and 14 eggs and 3 males and 2 females were dead after 3 days; at 40°C 2, 2 and 0 eggs were laid and 14 males and 6 females were dead after 1 day, 15 males and 11 females after 3 days, and all were dead after 5 days; at 44°C, no eggs were laid and all lice were dead after 1 day. Thus most eggs were laid at 35°C.

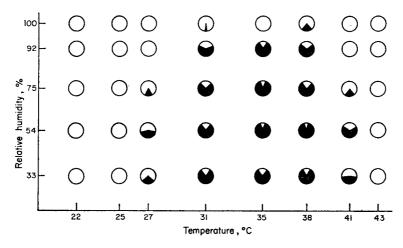


Fig. 7. Percentage hatch of eggs of *C. columbae* maintained at constant temperatures and relative humidities. The black area within each circle represents the percentage which hatched.

Two groups of 10 females were placed in glass tubes and exposed to 54% r.h. at 15°C for 7 days when they were given fresh feathers and exposed to 35°C for 8 days, after which they were again given fresh feathers and exposed to 26°C. Two other groups were exposed for similar periods to 26°C, 35°C and finally 26°C, and two more groups were exposed to 35°C for the whole period. The number of eggs laid by the two groups exposed to each treatment were similar, and Table 3 shows the total number of eggs laid. Oviposition ceased at 15°C, and fewer eggs were laid at 25°C than at 35°C.

Colpocephalum turbinatum. Colonies of this louse were established in the laboratory successfully, and the full biological data will be described in detail elsewhere (Nelson, unpublished data).

Temperatures (°C) to which groups of 20 females were exposed				Number of eggs laid and surviving famales						
0–7 days	8–16 days	17-25 days	0–7 days		8–16 days		17-25 days		Total number of	
			Eggs	22	Eggs	99	Eggs	φφ	eggs laid	
15	35	26	1	20	126	20	39	18	166	
26	35	26	21	20	75	17	30	14	126	
35	35	35	57	20	50	19	66	16	173	

Table 3—Influence of temperature on oviposition of Columbicola columbae

Colonies could only be maintained by supplying body feathers as the lice fed on the fluff (Fig. 5). In heavy infestations on pigeons the fluffy zone of virtually all of the feathers of the vent region were eaten However adults also eat their own eggs and nymphs causing substantial reductions in numbers in cultures

Most eggs were laid from 32–37°C but few were laid at 30 and 40°C. The eggs developed and hatched most satisfactorily from 32 to 37°C, particularly at 37°C at a r.h. of 75%. None hatched at 40°C.

DISCUSSION

The temperature requirements for oviposition and egg development fell within the range 32–40°C for all species of lice whether eggs were found on the body or wing. Such temperatures are found on the body of the pigeon and on the wings when they are folded against the body. The fluffy zone of the body feathers was a source of food for the four species of lice, and appeared to be the sole diet of the ischnoceran lice C. b. compar and C. columbae. The amblyceran lice however supplemented this diet; H. lata fed on blood probably derived from the papillae of the body feathers of the sides, back, and vent where they appeared to congregate, and C. turbinatum by predation on its own eggs and nymphs. In view of their feeding behaviour all of these species are body lice. Thus classifying avian lice as head, body or wing lice can be biologically misleading.

The number of lice on pigeons invariably increased following reduction of the efficiency of preening by clipping the upper bill, as has been reported for other species of birds when the bill is damaged (Kartman, 1949; Rothschild & Clay, 1952; Baum, 1968). Furthermore the distribution of the nymphs and adults over the body became more widespread. However the distribution of eggs did not change rapidly. The eggs of C. turbinatum were still only found on the primaries and their overcoverts, the alulae and the secondaries of the wing. Those of H. lata spread over the head and then extended down the neck from the head. Those of C. b. compar were not laid on the primaries, secondaries and undercoverts, and the numbers of C. columbae increased more rapidly on the wings. Preening apparently removed nymphs and adults and this controlled numbers but lice selected areas for oviposition where eggs appeared to be secure from preening. The selection of oviposition site was not associated with a specific attribute of the feather in a particular region as all lice would lay eggs on other types of feathers where no alternative was available. C. b. compar laid eggs on all parts of a body feather when exposed to constant temperatures but on a temperature gradient laid eggs in the 39-41°C zone. This attraction to warmth would lead the louse to the silky zone of a body feather on a pigeon. H. lata was clearly selecting the head of the pigeon, and only laid eggs on body feathers when numbers increased greatly. C. columbae laid eggs principally on the undercoverts of the wings, and C. turbinatum on the primaries, secondaries and overcoverts of the wings. The absence of their eggs from similar situations on the tail is probably because the temperatures are usually too cold for oviposition, as the oviposition site lies outside the insulating blanket of air trapped around the body of the pigeon. In cultures, eggs were attached to any feather and even to the side of the glass vial. The site of egg laying appeared to be closely associated with the behaviour of the adult louse prior to the onset of oviposition. C. columbae may be seen resting in the furrows between the barbs of the primaries and secondaries (Stenram, 1956), and C. turbinatum also rests within the calamus. It thus would appear that preening has influenced the behavioural evolution of these lice.

C. compar is a small louse, slow moving and found mainly in the fluffy zone of the ventral side of body feathers where it feeds near to the rachis. Eggs are laid on the same feather in the silky zone near the skin. When the feather on which a louse is present is touched or disturbed the louse frequently drops from it to another, a behaviour which may well allow it to avoid preening. H. lata is a large stout louse which moves rapidly over the skin between the feathers and feeds in the fluffy zone but attaches its large egg to the ventral surface of the feathers on the head, several eggs to each feather. C. columbae is a large thin louse which is morphologically adapted to rest in the furrows of primary and secondary feathers and to lay eggs in the furrows of the undercoverts. Furthermore it grasps the barbules of feathers firmly with its mouth parts, which is probably another adaptation to survive preening. It

feeds on body feathers, usually those of the forepart of the body as suggested by Martin (1934), Eichler (1939) and Ash (1960). C. turbinatum is a small louse which runs rapidly along the calamus and rachis of feathers. It shelters inside the calamus of primary and secondary feathers and in the furrows between the barbs where it lays its eggs. It feeds mainly on the body feathers of the vent region which is adjacent to the feathers of the wing and tail where it rests and shelters.

All of these species of lice of the pigeon feed on the fluffy part of the body feathers so that their gross morphological differences can only in a small way be due to adaptation for feeding. Rather it would appear that the selective pressure of preening by the pigeon has played the major role, and the morphological and behavioural adaptations of the lice ensure that they and their eggs survive this type of predation.

Acknowledgements—The assistance of Gundula Shirley in the early stages of this study is particularly gratefully acknowledged, as is the technical assistance of Katherine Brown, Janice Edwards and Glenis Wellings. The work of Dr. B. C. Nelson was supported by a National Institutes of Health Fellowship No. 1-F2-GM-36, 584-01 and 5-FO2-GM36, 584-02 from the National Institute of General Medical Sciences.

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