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STUDIES ON POPULATIONS OF HEAD-LICE (*PEDICULUS HUMANUS CAPITIS*: ANOPLURA)

IV. THE COMPOSITION OF POPULATIONS

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(With 4 Figures in the Text)

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The material

The previous papers in this series (Buxton, 1936, 1938*b*, 1940*a*) have described a method by which head-lice may be removed from a crop of hair and counted. In those papers the material was considered from the human point of view, that is to say, material from seven or eight different places was discussed: it yielded information about the incidence of infestation and its relation to the human being's age, sex and race, also to the season of the year, etc.

So far no attention, except for one brief note (Buxton, 1937), has been given to the strictly entomological side of the matter, and we will now consider the composition of the louse populations. For each infested head we know the total number of lice and the number of the males, females[1] and larvae. In dissolving the hair eggs are destroyed and we know nothing of their numbers. One assumes that all the insects in the crop of hair were alive at the time the head was shaved: this entails a small error, for it is evident that at death a louse might remain for some time among the hair. This source of error does not appear to be important, for if one examines infested heads one seldom finds a dead louse among the hair. The large collection of specimens from Cannanore has been preserved so that one could also identify and record the separate larval instars: this is laborious and has in fact only been done for a part of the material. But in dealing with specimens for the other localities no attempt was made to identify separate larval instars. It will therefore be seen that the material available may be expected to yield information about the proportion of the sexes in natural populations and the number of young per parent: it may also be possible to obtain some indirect information about larval mortality.

[1] It will be remembered that the hair is dissolved and only the cuticle of the lice left for counting and examination, which is generally done at a magnification of ×8. It is possible that specimens showing a minor degree of intersexuality may have passed undetected. No gross intersexes, such as those figured by Keilin & Nuttall (1919), have been seen, and I am confident that they could not have passed unobserved.

The mass of information which is available is considerable, for it includes every infested head in the material which was the subject of the three previous papers. Even if we exclude the data from Jerusalem for reasons already explained (Buxton, 1938*b*) we have a total of 858 infestations for study. As Table 1 shows, almost exactly two-thirds of these contained only from 1 to 10 lice, nearly one-third from 11 to 100 and a very small proportion more than 100 lice.

One is probably not justified in lumping together facts collected from the different places. If we are to study the places separately we need give little attention to Sokoto and Nairobi, from which small numbers of infested heads and of lice were received: the collection from Lagos was derived from few heads but it contained larger numbers of lice: the collection from Colombo was extensive, but for reasons already given (Buxton, 1938*b*) it is necessary to disregard the number of larvae, so that it is only valuable where adults are concerned: one is left with the collections from Kakamega and Cannanore, both of which were well collected and contained large numbers of infested heads and of lice: it will be seen that the total number of heads from Cannanore exceeds the whole of the rest of the material. It has been shown (Buxton, 1940*a*) that infestation rates are very different in religious communities in the Cannanore material: it therefore seems best to confine one's work to the Hindus, discarding Moslems and Christians: one loses only sixty-six (12·1 %) infested heads.

This is perhaps a convenient place for recording that a heavily infested shirt from south London was found to contain 369 adult body lice, of which 177 (47·9 %) were males.

Previous writers have had relatively so little material that I have not attempted to compare their results with my own. The results of examining a few populations of *P. humanus* are given by Nuttall (1917, 1919) and by Awati (1922).

Proportion of the sexes

It will be remembered that in certain strains of lice there is a tendency to produce families which are nearly or completely unisexual. This perhaps explains the remarkable disparity between the sexes which may be observed among the lice on a single head, particularly when the total number is low: it is reasonable to attribute this disparity to a head being nearly or entirely populated by the progeny of one pair of lice. The following examples, which are extremes rather than normals, show the number of adult males and females that have been found on single heads from several parts of the world: Colombo, 257:96, 447:116, 11:30, 28:7, 0:7; Lagos, 14:3, 3:17; Kakamega, 5:1, 0:5, 15:5, 0:7, 7:16, 116:198, 5:24.

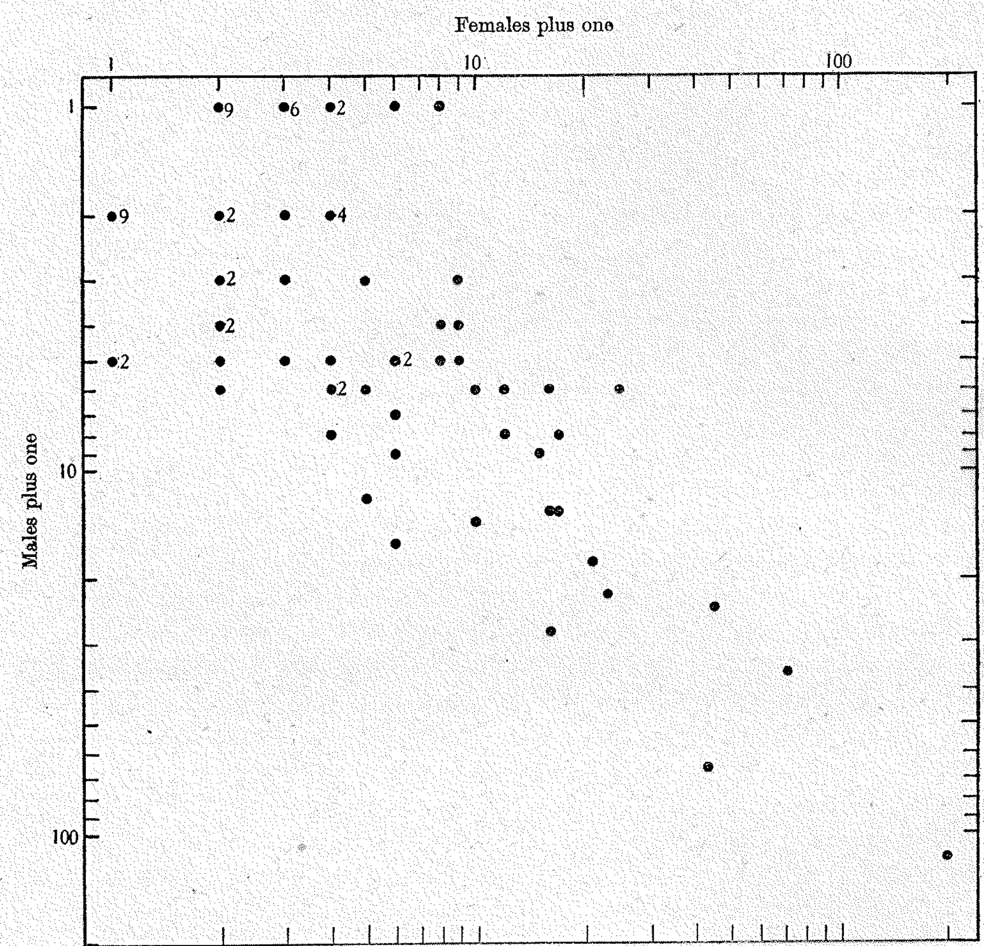

Fig. 1. Showing the number of male and female lice on separate heads from Kakamega, Kenya. The scale is doubly logarithmic for the sake of compactness: it has been necessary to add one to the number of males and females on each head, for there are a considerable number of zeros (e.g. heads with 2 males, 0 females), and zero cannot be shown on this scale.

The same disparity between the sexes in large numbers of heads is also shown in Fig. 1, which gives the number of male and female lice in all the heads from Kakamega in which adult lice occurred (the total number of heads is seventy-eight, not the ninety shown in Table 1, because twelve infested heads contained only young lice). A similar distribution (Fig. 2) shows the numbers

of males and females in 125 infested heads from Colombo. Figs. 1 and 2 show that, particularly when the total number of lice is low, many populations contain only adults of one sex. If one takes the ninety populations from Kakamega, there are thirty-nine in which the total number of lice (including larvae) was ten or less: in these both sexes were present in six (15 %) only, one sex in twenty-two (56 %) and larvae only in eleven (28 %). As a contrast, in the fifty-one heads which contained more than ten lice, both sexes were present in forty-three (84 %) and one sex in eight (16 %).

Table 1. *Showing the total number of populations of head-lice available for study, and the number of them in which there were* 1–10, 11–100 *or over* 100 *lice*

Place	Total infested heads	Heads with 1–10	Heads with 11–100	Heads with 101 and over	Percentage distribution 1–10	Percentage distribution 11–100	Percentage distribution 101 and over
Lagos, Nigeria	21	7	9	5	—	—	—
Sokoto, Nigeria	42	31	9	2	—	—	—
Nairobi, Kenya	37	24	12	1	—	—	—
Kakamega, Kenya	90	39	42	9	43·3	46·7	10·0
Colombo, Ceylon*	125	81	35	9	64·8	28·0	7·2
Cannanore, South-west India	543	356	173	14	65·6	31·9	2·6
Total	858	538	280	40	62·7	32·6	4·7

* Adult lice only (see Buxton, 1938*b*).

In a group of heads, for instance all those from one place, the correlation coefficient (r) is the most convenient way of expressing the degree to which the numbers of males and females are related. In calculating this coefficient one must exclude those heads which contained only larvae (without males or females). The values of n are therefore less than those given in Table 2. The following coefficients have been calculated:

Place	n	r	S.E.
Kakamega	78	0·93	0·11
Cannanore (Hindus)	461	0·80	0·05
Colombo	125	0·83	0·07

Table 2. *Giving the numbers of adult lice and proportion of males in all infested heads from certain places*

Place	No. of infested heads	Total lice Adults	Total lice Males	Males as % adults	Diff./S.E.
Lagos	21	516	293	56·8	3·1
Sokoto	42	96	37	38·5	2·2
Nairobi	37	72	30	41·7	1·4
Kakamega	90	1231	528	42·9	5·0
Colombo	125	4180	2346	56·1*	7·9
Cannanore	543	2333	1082	46·4	3·5

* But see Table 4.

It can be seen (Fig. 1) that the correlation is approximately linear in the figures for Kakamega, and we have no reason to think that it is not linear for Cannanore. As to Colombo, it is known that the proportion of males increases with increasing density of population (below), so that the correlation is not linear, and one would use the coefficient with some hesitation. It need hardly be said that all these coefficients are "significant" (P is much below 0·01 in each case). My personal feeling is that they are surprisingly high, having regard to the erratic ratios observed in some heads.

For purposes of comparison one needs some expression of the proportion of males to females, which may be recorded in a number of different ways. The percentage distribution, i.e. the number of males and females per hundred adults, seems best, because it is the easiest for the ordinary person to grasp: it is sufficient to quote one percentage (the male), the other being obtainable by subtraction.

Though very unequal numbers of males and females may occur in a family, or in the lice on a single head, one might perhaps expect the numbers to approach equality in a group of heads from one place, but this is not so. If one adds together all the figures from each separate locality one obtains the facts given in Table 2: two things are evident, either sex may predominate, and the divergence from equality (50 % of each sex) is often large. The "significance" of this divergence may be tested by taking the difference of the actual percentages from 50, and the standard error of this difference. It is found that in the small sample from Nairobi the difference is not certainly significant: but in the other samples the difference is two or more times its S.E., so that one concludes that it is not due to a sampling error.

One may enquire whether the proportion of the sexes in a family, or in a wild population of *Pediculus*, is entirely determined by the sex chromosomes; or whether some environmental factor produces a mortality which is differential in respect of sex, or even causes a reversal of sex early in the individual's life. (For information relating to insects in general, see Wigglesworth, 1939, p. 404, and references there quoted: also Holdaway, 1932; Holdaway & Smith, 1933.) There are several environmental factors which might perhaps be effective in *Pediculus*.

Type and quantity of hair. One would suppose that the type of a man's hair (length, straightness, etc.) would be an important factor in the life of the head-louse. Probably, therefore, there is a great difference between life on an African scalp (with 5–10 g. of crinkled curly hair) or on a scalp in Ceylon or South India (with 10–30 or even 50 g. of nearly straight hair). But it does not seem that this difference affects the sex ratio: we find that among Africans the percentage of male lice was 56·78 at Lagos, 42·89 at Kakamega, 38·54 at Sokoto: among Asiatics, it was 56·12 at Colombo (but see below) and 46·38 at Cannanore (Table 2).

It seems probable that the length of a man's hair is an important factor in the life of the head-louse. We cannot measure the length, particularly in hair which has been shaved and sent in by post, but measurements of weight of the

crop of hair are available, and it has already been shown (Buxton, 1940*a*) that this is an important ecological factor. The facts from Kakamega, and from Cannanore (Hindus only), have been tabulated to show percentages of male lice in groups of men with different weights of hair. The figures (Table 3) do not indicate any relation between the proportion of males and the hair weight. Similar figures have been worked out for all the other localities: they support this conclusion.

Table 3. *Showing the numbers of adult lice and the proportion of males in infested heads from Cannanore and Kakamega, the heads being distributed according to weight of hair*

N = no. of infested heads, ♂♀ = total adults, % = percentage of ♂♂ in total adults.

Cannanore (Hindus) Material	N	♂♀	%	Kakamega Material	N	♂♀	%
Hair: Up to 9·9 g.	56	111	40·5	Hair: Up to 5·0 g.	33	179	37·4
10–19·9 g.	153	377	43·5	5·1–10 g.	37	460	46·1
20–29·9 g.	118	480	52·1	Over 10 g.	20	592	42·1
30–49·9 g.	108	638	46·4	All weights	90	1231	42·89
Over 50 g.	26	340	48·8				
All weights	461	1946	47·3				

Density of louse population. The number of lice per head tends to be positively correlated with the weight of the host's hair, which has just been shown not to have any regular relation to the insect's sex ratio. It therefore seems probable that the density of the louse population would have no influence on the sex ratio. The facts for Kakamega and Lagos have been worked out, and show no relation between the number of females per head (used as a measure of density) and the percentage of males. The figures hardly justify publication, and similar data from other places have not been tabulated.

The material from men in jail at Colombo, Ceylon, stands by itself because the numbers of lice were unusually high on certain individuals. It will be remembered that 125 heads containing adult lice were examined, and that among them nine contained more than 100 adults, the larvae being uncounted for a reason already given (Buxton, 1938*b*). The proportion of males and females in the 125 is shown in Fig. 2. In Table 4 the figures are tabulated, to show the percentage of males at different densities of population. As to the low proportion of males (30·30 %) in the least dense infestations, I have no explanation to offer, and have not observed the same phenomenon in material from other places. In heads containing from three to twenty-five adult lice the proportion of males is between 45 and 46 %, and we may perhaps regard this figure as normal for the area. When the adult lice are from 26 to 100 per head (and this would be regarded as a heavy infestation in most places) the proportion of males rises, and it rises still more in the nine heads in which the total number of adult lice exceeds 100. The rise in the proportion of males is remarkable, and unquestionably significant.

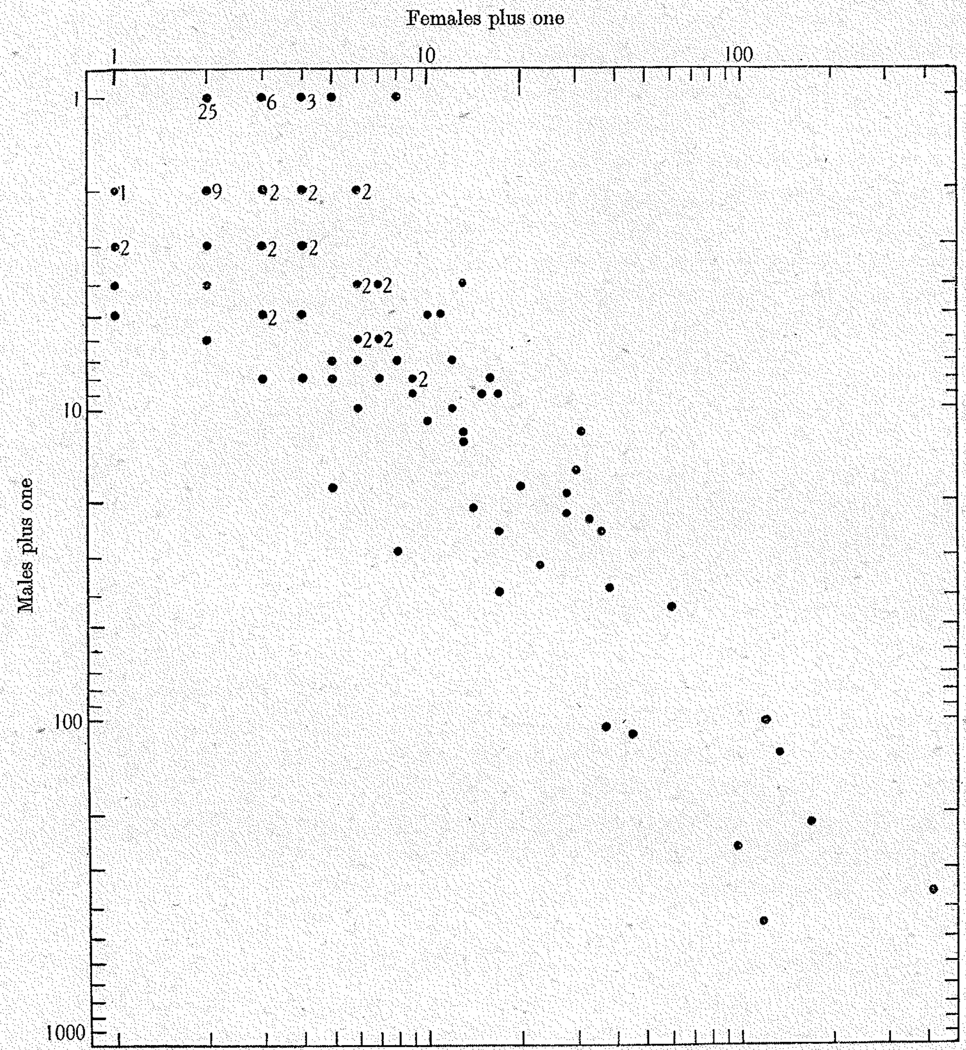

Fig. 2. Showing the number of male and female lice on heads from Colombo, Ceylon; for scale and conventions see Fig. 1.

Table 4. *Showing the percentage of males in populations of lice from Colombo*

Adult lice per head	No. of heads	Total lice: Adults	Total lice: Males	Males as % of adults
1–2	49	66	20	30·30
3–10	32	186	85	45·70
11–25	22	364	166	45·60
26–100	13	617	307	49·76
101 and over	9	2947	1768	59·99
All	125	4180	2346	56·12

It seems probable that this increase in the proportion of males, which is only observed when the density of lice is remarkably high, is explained by certain experiments which have been recently published (Buxton, 1940*b*, Table 2): it was shown that if one kept one young female in a box with six or more males, her life was materially shortened and her daily production of eggs greatly reduced: in a series of experiments the mean life of the female was 8·75 days, the normal being 30·56, the life of the males not being reduced. Clearly then the effect is not due simply to crowding, but to the effect of many males on one female: presumably her death is due to repeated pairing, or to the males' violent attempts to pair. One is probably justified in thinking that something similar occurs in nature when the density of the population has passed a certain point: the figures from Colombo (Table 4) seem to indicate that a differential mortality of the females begins when the number of adults per head is between 25 and 100, and that it is greatly increased when the total passes 100. In effect this gives the population an internal mechanism which prevents it from increasing beyond a certain point; the mechanism is that when the chance of the sexes meeting is very high, the males begin to have an unfavourable effect, therein resembling a predator which is more destructive when the density of prey is highest.

Certain biological factors. As already reported (Buxton, 1940*b*), experiments have been performed in order to discover whether partial starvation, or crowding in early larval life, affects the proportion of the sexes. The experiments were not conclusive, but give no grounds for thinking that any such result occurred. It is difficult to suppose that in nature either starvation or crowding could have any such effect.

In certain other insects, the production of males and females is determined by parthenogenesis, or delayed fertilization, or the sex ratio of the offspring changes towards the end of the mother's life. None of these causes are operative in *Pediculus*.

Climatic factors. In experiments and in nature, lice are maintained on the surface of the body, that is to say under equable conditions of temperature and humidity. But in spite of this, widely divergent sex ratios may be observed; in experiments, one may even have all male and all female families at the same season. It seems to follow that temperature and humidity cannot be effective in altering the proportion of males and females.

Conclusion. From the fact that, under uniform conditions of breeding, one may obtain unisexual or mixed families it seems evident that the sex ratio is determined by the chromosomes alone. It seems therefore to lie with the cytologists to provide us with an explanation of what occurs. The early work of Doncaster & Cannon (1920) and Cannon (1922) will serve as an introduction to the subject. No evidence has been found that any environmental factor has any effect upon the sex ratio (save in the exceptional case where a female encounters a male extremely frequently).

Proportion of larvae and adults

In considering the relation between number of larvae and adults it seems sufficient to limit the enquiry to larvae and females. The gross figures are set out in Table 5.

Table 5. *Showing the material available for study, and the numbers and proportions of females and larvae*

Place	Total infested heads	Lice: Females	Lice: Larvae	Larvae per female	S.E.
Lagos	21	223	2062	9·25	0·62
Sokoto	42	59	493	8·36	1·32
Nairobi	37	42	459	10·93	1·24
Kakamega	90	703	4409	6·27	0·48
Cannanore	543	1248	6774	5·43	0·41
Total	733	2275	14197	6·24	0·08

In general, one may say that the facts about larvae and females resemble those already studied about males and females. Individual heads depart greatly from the mean, as one sees in Fig. 3, which gives the number of larvae and females in eighty-five heads from Kakamega. In this group the mean number of larvae per female is 6·27, but in several heads the ratio is under three or over ten. One may show this in a different way by grouping all heads which contain a particular number (0, 1, etc.) of females. The sort of result one obtains is shown in Table 6, which gives the data for heads from Cannanore. The scatter in each group is so great that the standard deviation generally exceeds the mean. In considering such facts as these, it would be wrong to think of the lice on a head as a family. If one finds a female and some larvae they may be parent and children, or they may be unrelated, or the female may be the elder sister (newly emerged) of the larvae. This probably helps to explain the great diversity which is found between heads.

Table 6. *Showing the numbers of larvae per head in all heads containing no females, one (two, etc.) females, from Cannanore*

No. of females per head	No. of heads	Larvae per head: Max.	Min.	Mean	S.D.
Nil	211	45	0	4·03	6·58
One	153	37	0	4·48	7·18
Two	53	75	0	12·79	14·81
Three	34	75	0	12·59	15·67
Four	15	73	6	21·93	18·09
Five	19	87	0	25·11	21·88
Six	8	65	14	33·87	54·87

None the less, though there are many aberrant members in the group, there is a clear tendency for the numbers of larvae and females to be related (Fig. 3). For Kakamega the correlation coefficient is $0·87 \pm 0·11$: for Cannanore it is $0·72 \pm 0·04$. One feels some surprise that the coefficients are so high.

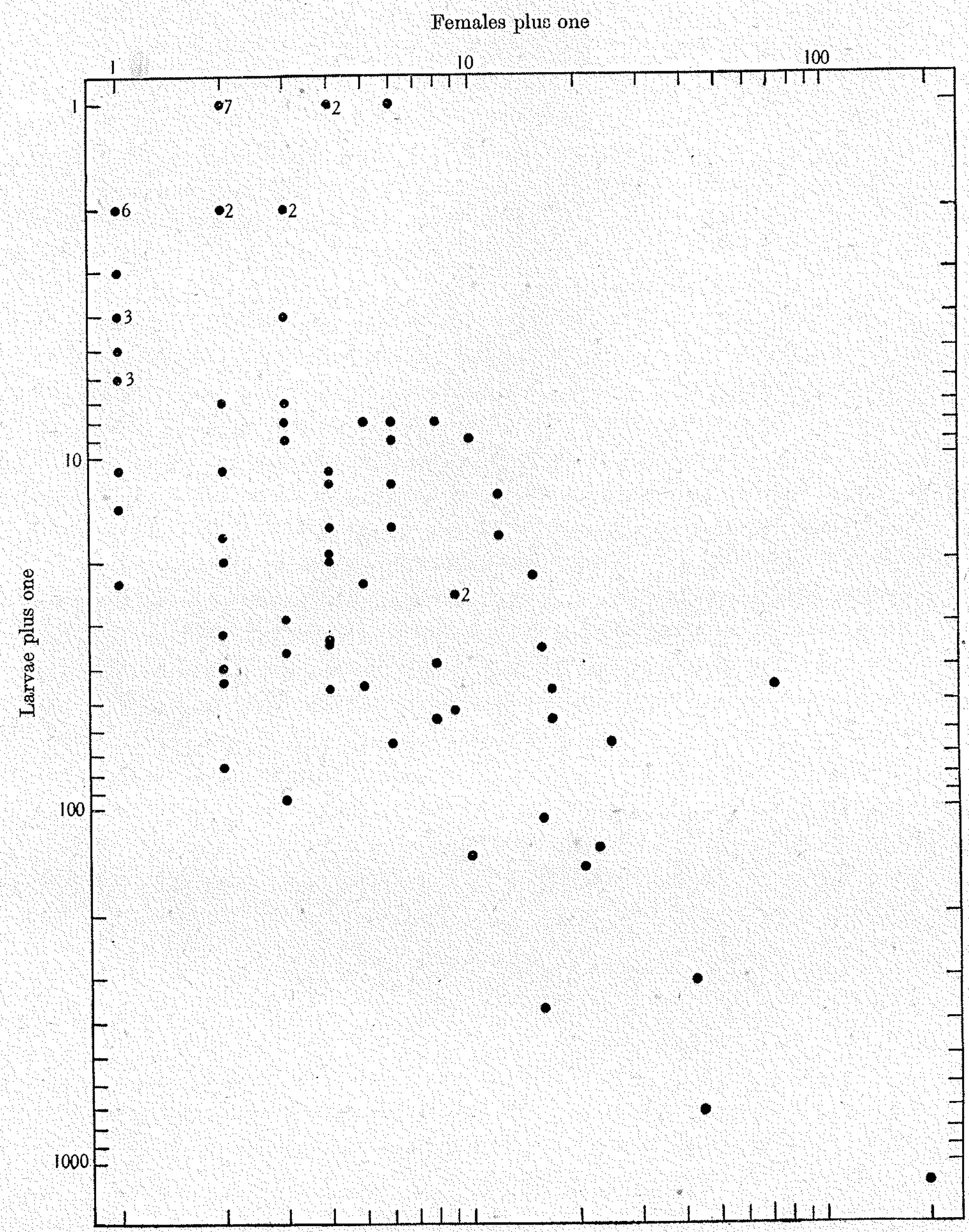

Fig. 3. Showing the number of females and larvae on separate heads from Kakamega, Kenya; for scale and conventions see Fig. 1.

If one considers the mean number of larvae per female, one finds large differences between different localities. At Lagos, Sokoto and Nairobi, the mean lies between 8 and 11; but at Kakamega it is 6·3, and at Cannanore 5·4 (Table 5). Between any two of the first three places the difference cannot be regarded as significant; all other differences, including that between Kakamega and Cannanore, exceed twice their S.E. and are significant.

One is inclined to suppose that some environmental factor may account for these great differences in the number of larvae per female, in different samples. Our general knowledge of the biology of *Pediculus* suggests several factors which might be effective.

Type and quantity of hair. We have already seen that the difference between Asiatic and African hair does not seem to be associated with any constant difference in sex ratio. Similarly, it appears not to affect the number of larvae per female: for instance, though the number is high in three African collections (Lagos, Sokoto, Nairobi) it is low at Kakamega (Table 5).

Weight of hair, already known to be a variable important to the louse, might have its effect on the number of larvae per female. For this, the best available figures are those from Cannanore, for the range of weight of hair is so great. The figures (Table 7) at first sight seem to show that as weight rises there is a fall in the number of larvae per female, but the correlation coefficient (−0·69) might occur by chance about one time in ten, and cannot be regarded as significant. One notices that in the first weight group (up to 9·9 g.) the number of larvae per female is very high.

Table 7. *Showing the relation between weight of hair, and the number of larvae per female, in material from Cannanore (Hindus only)*

Hair weight g.	No. of infested heads	No. of lice: Female	No. of lice: Larvae	Larvae per female
Up to 9·9	56	66	569	8·62
10–14·9	75	77	453	5·88
15–19·9	78	136	646	4·75
20–29·9	118	228	1399	6·14
30–39·9	63	231	1167	5·07
40–49·9	45	111	487	4·39
50·0 and over	26	174	785	4·51
Totals	461	1023	5506	5·38

It is hardly likely that samples of hair from Africa would show a relation between weight of hair and larvae per female, for the range of weight of hair is not great. The figures for Kakamega are:

Hair weight g.	Heads	Females	Larvae per female
Under 5·0	33	112	9·64
5·1–10·0	37	248	4·50
10·1 and over	20	343	6·35
All weights	90	703	6·27

Figures for Sokoto, Nairobi and Lagos show a similar absence of relation. In the above figure for Kakamega, the number of larvae per female is high in the first weight group, as it is at Cannanore (Table 7); but it is not high at the other African localities.

Density of louse population. The data from Cannanore have been divided into groups, containing 0, 1, 2, etc., females: there is no evidence that the number of larvae per female rises or falls with the number of females. One should, however, remember that at Cannanore the density is never very high: only fourteen heads were found in which the total number of lice exceeded 100. Colombo is the only place in which I have found considerable numbers of larger populations of lice; unfortunately, the figures for larvae at Colombo must be disregarded as already explained (Buxton, 1938*b*).

It is also possible that the number of larvae per female might be less in those heads in which there is an excess of males. Some time has been given to considering this, the Cannanore material being sorted according to whether the number of males was above, equal to, or less than the number of females. No relation was discovered between masculinity and the number of larvae per female.

Climatic factors. It will be remembered that the temperature and humidity in the hair are much more stable than they are in the general atmosphere. But, on the other hand, weather and season have such great effects on man, and on his occupations, that they might also, though indirectly, affect his parasite. Indeed, it has already been shown that the rate of infestation in certain places (Sokoto, Kakamega, Agra and perhaps elsewhere) is to some extent influenced by season (Buxton, 1938*b*), though we do not yet know what elements in climate are effective.

One might therefore find that the season or climate would cause alterations in the ratio of larvae to females (either by an effect on births, or on larval deaths). But a general consideration of the gross figures in Table 5 does not give much ground for thinking that this is so: the number of larvae per female is not significantly different in Lagos which is damp and equatorial and Sokoto which has a monsoon climate, with a short very wet season and a long rainless period. Moreover, one sees that though the climates of Nairobi and Kakamega (both in Kenya) are not unlike, the ratios of larvae per female are quite different (10·93 and 6·27). Prima facie, it seems that climate is not likely to be a major factor.

One may go rather further, taking a relatively homogeneous group such as the Hindus at Cannanore, and searching for a seasonal change in the number of larvae per female. The most striking seasonal change in the climate of the Malabar coast is in the rainfall, which is very heavy from May to October, and nil for the other six months. The Hindus show the following figures:

Months	Females	Larvae	Larvae/♀
May to Oct.	412	2202	5·34
Nov. to April	610	3305	5·42

Similar figures have been worked out for separate hair-weight groups: even in this more homogeneous material no evidence is found that the number of larvae per female is consistently higher or lower at one season.

It will be remembered that in Sokoto the climate is sharply divided into wet and dry seasons, and that there is evidence that people are more often infested in the dry season (Buxton, 1938*b*). The total amount of material is not great, and (in any one age group) fails to show any difference in the number of larvae per female. From the figures from Kakamega one draws a rather similar conclusion. If one excludes males up to ten years old and all females, the following figures are obtained, the months June to October being the colder and wetter:

Months	Infested heads	Females	Larvae	Larvae/♀
June–Oct.	33	150	749	4·99
Nov.–May	33	492	3012	6·12

The difference in the number of larvae per female in the two seasons is not quite twice its standard error, and one cannot regard it as convincing.

Reviewing the data as a whole, one cannot say that a seasonal difference in the number of larvae per female is proved to exist at any of the places studied. But it seems probable that if an abundance of material were collected at some place in which the seasons are sharply contrasted, such a difference might be discovered. That would be of great interest, for it would point to factors which may influence the rate of increase of populations of lice in nature.

Proportion of the three larval instars

In *Pediculus* there are always three larval instars, and it is not difficult to distinguish them. The lice recovered from hair from Cannanore (but not from other places) have been preserved in spirit, and my colleague, Dr Haddow, undertook to examine a part of them, so as to determine what proportion of larvae belonged to each instar. The work is laborious, for every specimen must be put under the microscope, and a good many must also be measured. It was easy to distinguish first instars, by the short abdomen and the few setae in regular longitudinal rows on the dorsum of the abdomen. The second and third instars are less easy to separate. It was found most convenient to measure the third tibia; it has been shown that, at least in body-lice, this measurement gives a clear difference between instars. In the present material no doubtful cases were encountered; the absolute measurements were rather less than those published by myself, probably because the head-louse tends to be smaller than the body-louse in most respects. Occasionally, if the legs were bent or damaged, second and third instars were distinguished by points in the chaetotaxy (Buxton, 1938*a*).

After he had examined all specimens from the first fifty-one infested heads, Dr Haddow considered the results and desisted, for it seemed doubtful if the

labour was justified. These fifty-one heads were unselected: they were the first infested heads met with in the inquiry and were collected from May to August 1937. In them there were 142 males, 154 females, and 502 larvae, a total of 798. The larvae yielded the following data:

	Numbers	%
1st instar	218	43·4
2nd instar	189	37·7
3rd instar	91	18·1
Indeterminate	4	0·8
	502	100·0

The reduction from first stage to second is 13·3 %, from second to third 51·8 %. As we know that the length of life of the three instars is approximately equal, it is clear that the death-rate is very far from regular; indeed, it is four times as high in the third instar as in either of the other two. Moreover, the deaths occur during the course of the third instar: if they occurred at the beginning or the end of it (for instance at the final moult), that would not produce the figures obtained. As to the cause of these deaths, we are ignorant. It will be remembered that under experimental conditions, if body-lice are reared in boxes on myself, there is a high death-rate early in the first instar, and that this is believed to be due to artificial conditions (Buxton, 1940*b*). From this it is evident that the course of mortality among larval head-lice in nature and body-lice in boxes, is entirely different.

Perhaps I may set down a line of argument, which would lead to new and valuable conclusions, though it is not applicable to these figures. Let us suppose that we are dealing with some insect in which the number of instars is known and invariable, and that the length of time passed in each is also known: furthermore, on analysing a population, evidence has been found that mortality is at a steady rate through larval life (which it is not in *Pediculus*). We may represent the facts by a diagram (Fig. 4) in which each instar is shown as a rectangle, of which the base is proportional to the length of life of the instar: in the case

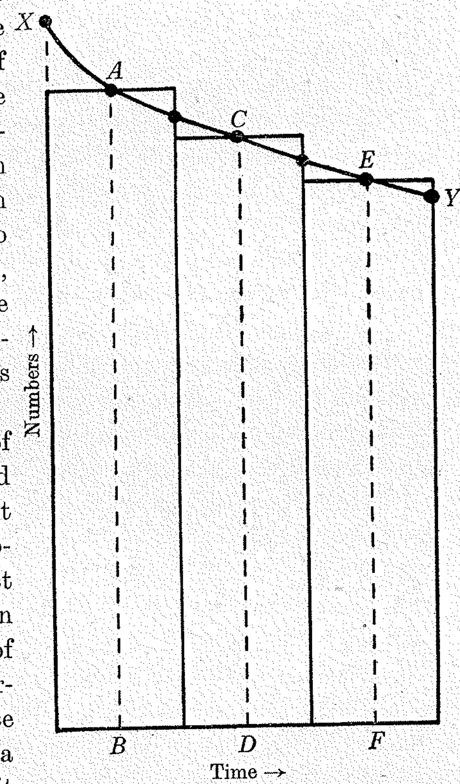

Fig. 4. Hypothetical case in which the three instars (shown as rectangles) are reduced by mortality at a steady rate.

chosen for illustration there are three instars, and their duration is supposed to be equal. If there are a large number of insects in each instar, then one may say that the average one is half-way through its life in that instar: the lines *AB*, *CD*, *EF* will therefore represent the numbers in each instar. But as the mortality is at a steady rate (by definition) these numbers fall on a geometrical progression. One may therefore extrapolate and find the points *X* and *Y* on the same geometrical progression. These points give one the number of first instars which succeed in hatching from the egg, and the number of last instars which reach the final moult. There are certain circumstances, depending on the nature of each case, under which those figures might point further to conclusions of value.

The line of argument appears to be of considerable potential value: it may be adapted according to the particular insect under study.

Discussion

The subject of insect populations is one to which many workers, in pure and applied science, will turn in the future: there are a number of possible ways of approaching it. A population is essentially dynamic, in the sense that it is always increasing or decreasing, and exhibiting change in the proportion of larvae and adults in it. But if one takes a large number of populations, as we have in this paper, one may think of them as static; for instance, in the village as a whole the lice will not be increasing, for the gain on one head will be offset by the loss on another. It seems therefore legitimate to study events at a particular moment, even though one knows nothing of what led up to them.

The author has had the good fortune to deal with an insect of which the biology is extremely simple and well known. Each race of *Pediculus humanus* lives its whole life in a single environment; in this environment, temperature and also humidity tend to be stable. There is one food only, human blood, for adult and larva, and the supply of this is for all practical purposes unlimited, so that there is no competition for food. A simple method has been evolved for collecting the hair from the people who are to be studied, and for separating the lice from it; complete crops of nearly 3000 people from several parts of Africa and Asia have been studied. In the present group of papers I have already reported on the human side of the question; for instance, the relation of infestation to the human being's age, sex, race, etc., and to seasonal factors (Buxton, 1936, 1938*b*, 1940*a*). In the present paper we turn to the entomological side of the problem, and discuss all the actual infestations, which number 858.

To sum the matter up, we have an unusually favourable field for study; the insect's life history is simple and well known; there is abundant material, and it has been studied and tabulated in a variety of ways. Indeed, the writer has had a very unusual opportunity of discussing the relation of a parasite to

a vertebrate host. What comes of it? Do any points of general interest come out of this solid effort?

This is not the place to summarize the first three papers, but it is appropriate to call attention to certain general points which have emerged from that work; there is a strong positive correlation between weight of hair (which is the best measure we have of length of hair) and infestation: there is a negative correlation with age, boys tending to be more infested than youths, who are more infested than men. It has been possible to formulate one general rule; if one takes a large group, such as all the heads from one place, and divides them into subgroups (e.g. by age, or weight of hair) then those subgroups in which the proportion infested is highest are also those in which the highest counts of lice are found.

Another general point is that though the biology of *Pediculus* is simpler than that of the great majority of insects, the distribution of lice among men is complex. This is probably due, at least in part, to the complexity of human affairs. We observe for instance that in one part of Africa, at Sokoto, infestations are commoner in the hot season, and in another part, at Kakamega, in the cool, wet season; the explanation of the anomaly may well lie in the agricultural or social customs of the people. In a similar way, one cannot doubt that if a man with the necessary ethnological knowledge were to study the distribution of head-lice among people in certain parts of Asia or Africa, he would reveal the extent to which it is influenced by such things as hair dressing and hair cutting, and by all the customs which bring certain members of society into contact with others. All those complexities wait to be discovered; they must be studied on the spot, not in London.

It seemed at one time that one might be able to deduce the approximate mortality among the larvae from the number of larvae per female. I felt that data relating to the body-louse (Buxton, 1940*b*) might be used, in the absence of figures about the head-louse. As the biology of the insect is simple, particularly in respect of temperature and food supply, one may suppose that the daily production of eggs is uniform; and as a large population (on many heads) is stable, the proportion of larvae to adults does not change. I then took particular values for the female's length of life and daily production of eggs (Buxton, 1940*b*), and made certain assumptions about the mortality of eggs and larvae. If we first consider a simple but unnatural case, and assume that there is no mortality in the early stages, also that the female lays nine eggs daily, the duration of the egg stage and also of larval life being 9 days, then there might be as many as eighty-one larvae per female alive, excluding grandchildren. It will be observed that this figure of eighty-one is not affected by the length of the female's life, except when the female's life is under 9 days. But it is evident that this simple case has no relation to reality. One has to suppose that a certain proportion of eggs and of larvae die; but we know nothing about the mortality in either stage, and we may not suppose that the death-rate is the same in the egg and larval stages. We are therefore left with three major unknown factors, which are independent of one another so far as we know, the mortality of the egg and that of the larva, and the mean reproductive life of the female. There are many different combinations of these three variables, though not an infinite number, which would produce a particular figure for the number of larvae per female. No further progress seems possible at the moment, though the matter can be taken up again when we know more about the quantitative biology of lice, particularly of the head-louse. Data on the mortality of eggs in nature or on the length of life of marked females would be of great value. There is, however, one general conclusion which may even now be drawn. We know that in a large group of heads the mean number of larvae per female is five or ten or some such figure (Table 5). This must imply a very large mortality in the eggs or the larvae; there must therefore be some cause of death which acts differentially on early stages. Further than that we cannot now go.

This series of papers may be concluded on a note of depression and humility. We have studied a very simple and well-known insect, and have looked at it in a new way. A large amount of material has been collected and analysed, and very little that is positive has been found. All through the four papers the writer has continued to report failure to demonstrate any relationship between infestation and some natural event which one would have supposed to be a relevant factor.

Summary

1. In three previous papers (1936, 1938*b*, 1940*a*) the author has discussed the distribution of head-lice among their human hosts, his material being nearly 3000 complete crops of hair. The present paper deals with the strictly entomological side of the inquiry, that is to say, with the study of the populations of head-lice themselves. The total amount of material is the lice from 858 infestations from six places; from each of four places there were less than 100 infestations.

2. In about two-thirds of the infestations there were ten lice or less, the proportion of low infestations varying considerably from place to place (Table 1). Infestations over 100 never formed more than 10 % of all the infestations in a place.

3. In a single head the proportion of the sexes is often far from equal; indeed, in light infestations it is common to find that all the adults are of one sex. Taking all the heads from one place, the total number of males and females differs significantly from equality, an excess of males occurring in one place, of females in another (Table 2). In all heads from one place the coefficient of correlation between the number of males and females is high, about 0·8–0·9. As the density of the louse population does not generally affect the

sex ratio, the correlation is approximately linear. But when the density is unusually high, as it is in some heads from Colombo, the proportion of males rises progressively. This is the only case known, in spite of much searching, in which sex ratio of the louse is affected by an environmental factor.

4. In the matter of the number of larvae per female, there are great individual differences between heads, though the coefficient of correlation, worked on all the heads from one place is as high as 0·7 or 0·9. Taking all the heads from one place, the mean number of larvae per female ranges between 5·4 and 10·9; many of the differences between places are significant. I have failed to find any explanation of these differences, and they do not seem to be affected by any environmental factor. The fact that the larvae are always more numerous than the females, indicates that there is a high mortality during the course of larval life; the author has failed to make a more precise estimate of the proportion which die.

5. A small part of the material was specially examined, and every larva referred to its instar. In this sample of 502 larvae it was found that the death-rate was higher in the third instar than in the other two, a state of affairs the reverse of what occurs in body-lice reared in boxes.

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