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OBSERVATIONS ON NATURAL POPULATIONS OF THE BODY LOUSE, *PEDICULUS HUMANUS CORPORIS* DE G.

BY

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OBSERVATIONS ON NATURAL POPULATIONS OF THE BODY LOUSE, *PEDICULUS HUMANUS CORPORIS* DE G.

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(With 6 Figures in the Text)

Introduction

The materials for this paper were obtained from three sources: (*a*) the examination, on successive occasions during the period December 1939–April 1940, of volunteer subjects, mainly from common lodging houses in east London, prior to their treatment with pediculicides, (*b*) the examination, during April 1940, of large numbers of men from common lodging houses, Salvation Army hostels, night refuges and other sources, in a search for further suitable subjects for control experiments, and (*c*) the study of the process of infestation of shirts issued to selected volunteers and worn continuously over a period of 10 days. The material from the first source is largely selective, since infested volunteers were specifically invited; that from the second source is more representative of the population of cheap hostels, since no emphasis was laid on the presence of lice, the men being induced to submit to examination by the offer of payment. It is, however, obviously not a random sample since it represents volunteers, and neither it nor the source (*a*) material should be used as a measure of the frequency or degree of infestation normal to the corresponding group of the city population.

The full records on which this paper is based are very bulky; they are filed at the Cooper Technical Bureau, and are available for reference by interested workers.

Altogether, 263 sets of under-garments were examined, of which 34, 13 %, were free of lice. The remaining 229 sets represent 151 men, some of whom were examined on more than one occasion (source (*a*) material). Of these 151, 15 % had counts, on first examination, of over 100 lice, 7 % over 250, and 3·3 % over 500, 2 being over 1000.

Definitions

'Environment': the term has been confined in this paper to the physical environment of the infested subject.

'Habitat areas': this term is restricted to the different areas of the garment surface defined in the text.

'Territory areas' consist of two opposed surfaces. The first territory area is comprised by the skin and the inside of the first garment, the second by the outside of the first and the inside of the second garment. The third area is regarded, for purposes of the present study, as being one surface only, since examinations of the outer clothing were not made.

'Migration' and 'invasion' distinguish between the movement of lice from the outer clothing and from the 'environment' respectively of the infested subject.

'Native' lice are those which have hatched from eggs laid on the under-garment in question.

The consistency of infestation of individuals

The louse counts obtained for common lodging-house inmates consist of two groups, (*a*) 'original' counts, i.e. the first count on each new subject, and (*b*) several repeat or 'initial' counts on some of the men over the next few months. Most of the records, in the latter group, are due to a series of counts on certain individuals who were used repeatedly for louse control experiments, 2–4 weeks being allowed to elapse between one experiment and the next. The first count for each successive experiment, prior to treatment of the subjects, has been taken as an 'initial' count.

It became evident during the examinations that the infestation of an individual, observed from time to time, tends to remain within a given order of magnitude—his louse population level. Naturally this consistency was liable to interruption, from such causes as a recent change of garments being examined, or a recent visit to the municipal delousing station, but it was usually possible to predict the infestation level on repeat counts. Table 1 gives the counts made on nine subjects who were examined on five or more occasions.

Since single abnormally large counts swamp the average for the remainder, and also because of the wide fluctuations at high densities of population, the standard deviation has also been calculated as that of the logarithms from the mean log (Williams, 1937, 1940). By this method, which uses the geometric mean, the individual groups of counts fall into more clearly defined classes than when the arithmetic numbers are used. The geometric mean is, however, in this case a less reasonable measure of central tendency than is the arithmetic mean (cf. subjects 4, 5 and 9); the variance in the groups has, therefore, been analysed for significance simply on the basis of deviation from the arithmetic mean. Even so, the value for Z is practically equal to its 1% point, i.e. there is a highly significant association between the individual and his louse counts.

The frequency distribution of natural populations

The distribution of infestation values is shown in Fig. 1. The distribution has been treated in three parts: from 1 to 30 in intervals of 5, from 31 to 150 in 10's, and from 151 to 500 in 50's.

The curves, if plotted with equal horizontal spacing from 1 to 500, would be of inordinate length. They have, therefore, been contracted progressively from left to right, by basing the horizontal spacing on the log of $(x+20)$, x being each successive point on the scale. (A scale based directly on $\log x$ causes an excessive disproportion between the initial and later spacings.) The scale still

Table 1

Subject	Dec.	Jan.	Feb.	Mar.	Apr.	Arithmetic mean	σ	Coefficient of variation	Geometric mean	Mean log $(x+1)$	σ
1	4 8	1 2	4	—	0	3	2·86	95	2·3	0·52	0·338
2	8 5	33 7	0	—	1	9	12·18	135	4·5	0·74	0·536
3	50 53	147 110	62	—	37	77	42·71	55	68·2	1·84	0·224
4	8 38	120 133	139	77	430	135	139	103	57·9	1·77	0·552
5	32	3 1	19	—	75	26	30	115	12·2	1·12	0·654
6	45	14 5 9	18 14	—	7	16	13·56	85	12·8	1·14	0·292
7	66	370 131	68	—	7 41	114	131	115	63·6	1·81	0·555
8	51	17 41	5	—	45	32	19·78	62	24·7	1·41	0·394
9	303	140 34	0	270	121	144	122	84	59·3	1·78	0·935

represents an arithmetic progression of values, but the curves are, as it were, observed in perspective.

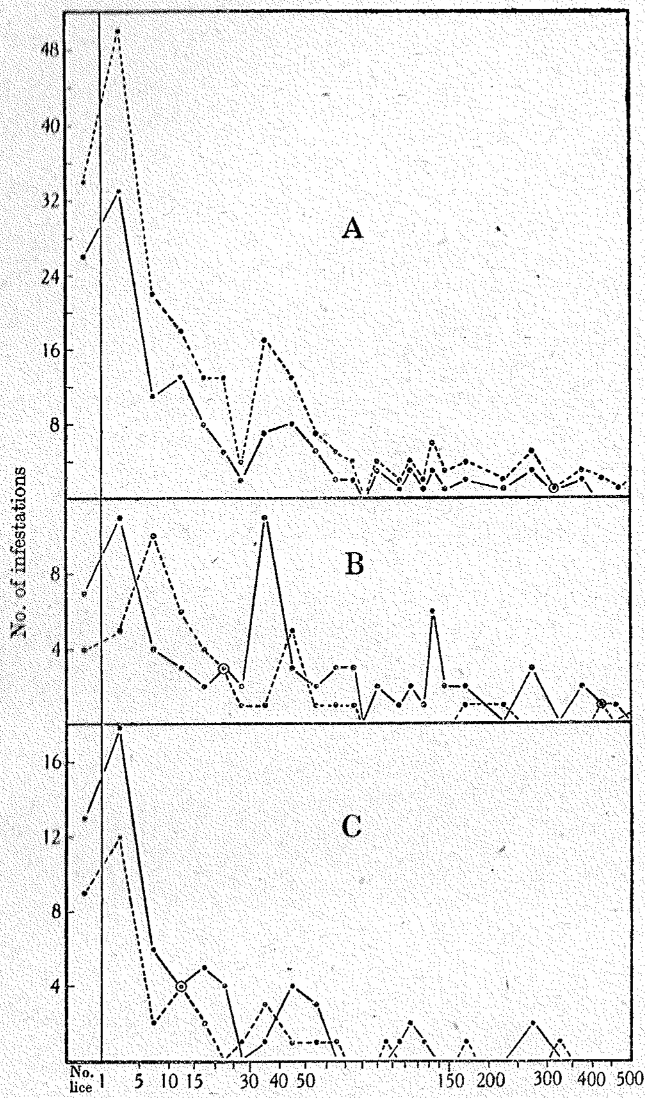

Fig. 1. The frequency distribution of infestations. A. From all sources: whole line, original counts; interrupted line, initial counts. B. Comparison of initial counts of two common lodging houses. C. Comparison of original counts of two Salvation Army hostels.

The frequency curve might be regarded as unimodal from inspection of the general curve (A) (cf. Peacock (1916) for body lice, and Buxton (1938) for head lice), but if the results from each community are treated separately, (B and C), at least two modes in the distribution are revealed. These do not necessarily coincide for different communities (cf. the two lodging houses examined (B), and the two Salvation Army hostels (C)), so that the troughs may be obliterated when records from different sources are combined.

In the present data, the frequency curve has the first peak between 1 and 10, the second between 30 and 60, and possibly other peaks at about 150 and higher. For convenience of handling, although the data for high infestations are scanty, the curve will be here regarded as having a third peak between 100 and 150. Hence the infestations have been divided into four groups, viz. infestations of 1–25, 26–80, 81–200, and over 200, each of which is regarded as corresponding to a mode.

Possible factors affecting the population level

The counts given in Table 1 were examined from the point of view of seasonal variation. A consistent tendency to decrease can be shown on treatment of the data, but is statistically insignificant.

In Table 2 the average infestation per man is given for men wearing different combinations of under-garments. One or two counts (e.g. one count of 2600 and one of 1217) were so high as materially to affect the averages; the geometric means of the groups are, therefore, also given. The infestation levels, judged by either measure, are independent of the number of under-garments worn. This conclusion is further supported by the distribution of the negative cases. Thus, if the number of under-garments affected the probability of a low infestation, the negatives would reasonably be expected to be most numerous in either the 'shirt only' group or the three garment group; actually they are relatively most numerous in an intermediate group (13 out of 57 examined).

The elements of a louse population

Adult-larval ratio

The adult-larval ratio for 16,527 lice examined is 1 : 3·6. Table 3 shows the relationship between population density and the adult-larval ratio. The densities are taken as those for the particular garment aspects in question, and not those for the subjects. The population values given are the totals for all garment aspects having populations within the appropriate limits.

Taking the total of all garments (columns 8–11): at densities of 1–3 the population on the inner aspects consists of approximately equal numbers of adults and larvae; the ratio increases as the density increases up to about 10 lice per garment aspect, after which it levels out at a range of 1 : 4 to 1 : 6, except for an occasional aberrant group. The higher larval ratios tend to occur at higher densities. If the ratios for shirts worn against the skin are considered, this relative increase of larvae at high densities becomes more apparent; from a range of between 1 : 4½ and 1 : 5½, the ratio suddenly increases, at densities of 563–1000 to 1 : 9½. Evidence is given later that at densities of over 1000 there may be a reversal of the ratio, due to exceptional conditions.

Table 2

	Shirt only	Shirt + one extra garment	Shirt + undervest	Shirt + undervest + one extra garment	Miscellaneous combinations of garments
No. of cases	119	22	44	14	6
Total lice	9672	1961	3690	895	323
Average	81	88	84	64	54
Geometric mean	10·72	23·99	10·72	27·54	13·18
Distribution of negative cases	17	1	13	3	—

Table 3

Population of garment aspect	Shirt against skin		Undervests		Second garment		Totals		Ratios	
	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside
1	5/7	10/14	6/2	7/7	5/7	6/4	16/16	23/25	1 : 1	1 : 1·1
2–3	9/12	13/31	10/7	16/17	12/15	12/17	31/34	41/65	1 : 1·1	1 : 1·6
4–6	27/48	28/47	13/24	18/34	14/19	15/12	54/91	61/93	1 : 1·7	1 : 1·5
7–10	20/59	42/105	3/30	4/10	3/30	3/7	26/119	49/122	1 : 4·6	1 : 2·5
11–18	37/204	58/117	19/125	21/50	8/33	—	64/362	79/167	1 : 5·7	1 : 2·1
19–32	79/414	38/94	34/120	25/51	21/76	7/21	134/610	70/166	1 : 4·6	1 : 2·4
33–57	104/481	98/235	35/168	4/35	—	—	139/649	102/270	1 : 4·7	1 : 2·7
58–100	149/451	34/128	8/90	—	—	—	157/541	34/128	1 : 3·5	1 : 3·8
101–178	205/1417	197/345	59/349	—	—	—	264/1766	197/345	1 : 6·7	1 : 1·8
179–316	236/1280	—	23/191	75/110	—	—	259/1471	75/110	1 : 5·1	1 : 1·5
317–562	309/1635	—	—	—	—	—	309/1635	—	1 : 5·3	—
563–1000	146/1378	—	155/600	—	—	—	301/1978	—	1 : 6·6	—
over 1000	206/844	—	—	—	480/645	205/230	—	—	—	—
Totals	1532/8230	518/1116	365/1706	170/314	543/825	248/291	—	—	—	—
Ratios	1 : 5·36	1 : 2·16	1 : 4·67	1 : 1·85	1 : 1·52	1 : 1·17	—	—	—	—

The highest larval ratio is found on the inner aspect of shirts worn against the skin (bottom row of Table 3). The rather lower ratio for undervests is probably due to many of these being of the sleeveless type, with few seams. On all garments the 'total' ratio on the outer aspect is approximately 1 : 1–1 : 2.

The ratios in the successive territory areas (obtained by adding columns 5 and 6 of Table 3) show the relative preponderance of adults in the outer two territory areas:

	Area 1	Area 2	Area 3
Totals	365/1706	713/1139	248/291
Ratios	1 : 4·7	1 : 1·6	1 : 1·17

Sex ratio

The sex ratio of 1786 adults sexed is 1 : 1·27 (males to females). On the successive aspects of two under-garments (excluding sleeveless vests and cases where two shirts were worn), the males are predominant on all aspects but the innermost:

	Males/females (inside + outside)	Ratios
Shirts against skin	505/746 + 226/205	1 : 1·48 + 1·1 : 1
Sleeved undervests	119/143 + 74/61	1 : 1·2 + 1·2 : 1
Shirts over sleeved undervests	29/16 + 19/15	1·9 : 1 + 1·3 : 1

Detailed examination of the data failed to reveal a shift of the sex ratio with increasing density, such as described by Buxton (1937) for exceptionally high densities of head lice.

The distribution of a louse population on the garment

Shirts worn against the skin

Table 4 summarizes the regional distribution of lice on 133 shirts worn against the skin. The habitat areas referred to are as follows:

Neck band (*Nb*).

Breast (*B*), areas of reinforced cloth where the shirt is buttoned in front, including the seams.

Shoulders (*Sh*), front and back seams of epaulettes, seam between the shoulder blades, and seam at head of sleeve except the 'armpit' area, including the area between these seams.

Armpits (*Ap*), the four-rayed star formed by the seams in the armpit, the area extending for approximately 1–1½ in. along each seam.

Side seams (*SS*), from the armpits to the bottom of the shirt.

General surface (*GS*); this is divided into top and bottom of the front (*Ft.Fb.*), and back (*Bt.Bb.*), by a line drawn at the level of the base of the breast area, and a corresponding line on the back surface.

Sleeve seams (*Sl.s*).

General surface of sleeves (*Sl.g.s.*), including cuffs and their seams.

On the inner aspect females are relatively most numerous in the armpits, which is a favourite oviposition area, and are also markedly preponderant (ratio 2 : 1) in the side seams. On the 'general surface' males were found to be predominant on the lower front portion, but not elsewhere. This difference was consistent for all densities below 300.

Table 4

Habitat	Total sexed (males/females/larvae)		Sex ratio		Total sexed and unsexed (adults/larvae)		Age ratio		Percentage distribution	
	Inside	Outside			Inside	Outside			Inside	Outside
Nb	6/14/111	2/1/20	1 : 2$\frac{1}{2}$	2 : 1						
B	30/37/397	19/17/80	1 : 1$\frac{1}{4}$	1 : 1						
Combined	36/51/508	21/18/100	1 : 1$\frac{1}{2}$	1 : 1	108/706	49/132	1 : 6$\frac{1}{2}$	1 : 2$\frac{2}{3}$	8	13
Sh: Right	31/58/742	7/5/28			113/897	15/28				
Left	51/75/897	9/6/33			156/1019	21/33				
Total	82/133/1639	16/11/61	1 : 1$\frac{2}{3}$	1 : 1$\frac{1}{2}$	269/1916	36/61	1 : 7	1 : 1$\frac{2}{3}$	23	7
SS: Right	30/56/731	6/8/54			136/996	17/58				
Left	22/46/666	6/12/44			97/861	23/49				
Total	52/102/1397	12/20/98	1 : 2	1 : 1$\frac{2}{3}$	233/1857	40/107	1 : 8	1 : 2$\frac{2}{3}$	22	10
Ap: Right	9/26/231	2/5/11			43/276	8/11				
Left	7/25/324	4/3/21			52/448	11/34				
Total	16/51/555	6/8/32	1 : 3$\frac{1}{4}$	1 : 1$\frac{1}{3}$	95/724	19/45	1 : 7$\frac{2}{3}$	1 : 2$\frac{1}{3}$	8	4
Sl.s.: Right	22/27/255	6/4/9			58/320	12/13				
Left	20/44/298	5/2/15			77/357	12/23				
Total	42/71/553	11/6/24	1 : 1$\frac{3}{4}$	2 : 1	135/677	24/36	1 : 5	1 : 1$\frac{1}{2}$	8	4
Sl.gs.: Right	14/26/145	8/6/34			68/200	18/42				
Left	20/23/173	11/18/36			60/213	34/42				
Total	34/49/318	19/24/70	1 : 1$\frac{1}{2}$	1 : 1$\frac{1}{4}$	128/413	52/84	1 : 3$\frac{1}{4}$	1 : 1$\frac{2}{3}$	6	9
GS: *Ft.*	22/34/533	11/9/82					1 : 9$\frac{1}{2}$	1 : 2$\frac{2}{3}$		
Fb.	54/49/272	31/24/103					1 : 2$\frac{2}{3}$	1 : 2		
Bt.	34/45/387	16/10/48					1 : 5	1 : 2		
Bb.	31/45/384	23/27/122					1 : 5	1 : 2$\frac{1}{2}$		
Unspecified	2/2/5	2/0/0								
Total, *GS*	143/175/1581	83/70/355	1 : 1$\frac{1}{4}$	1 : 1	489/1920	282/481	1 : 4	1 : 1$\frac{2}{3}$	25	53

Table 5

	Inner surface				Outer surface				Whole garment		
	Adults	Larvae	Age ratio	Total	Adults	Larvae	Age ratio	Total	Adults	Larvae	Total
Seam areas	840	5880	1 : 7	6720	168	381	1 : 2$\frac{1}{4}$	549	1008	6261	7269
General surface areas	613	2328	1 : 3$\frac{3}{4}$	2941	332	565	1 : 1$\frac{2}{3}$	897	945	2893	3838
Summation	1453	8208	—	9661	900	946	—	1446	1953	9154	11107
Seams as percentage of total	58	72	—	70	34	40	—	38	51	68	65

The proportion of lice on the inner and outer aspects, with different total densities of population, is as follows (expressed as the ratio outside/inside):

Density	1–3	4–10	11–18	19–32	33–57	58–100	101–178	179–316	317–562	Over 562	Total
Ratio	1 : 2	1 : 8	1 : 6	1 : 7	1 : 5½	1 : 4½	1 : 7	1 : 6½	1 : 7½	1 : 7½	1 : 6¾

Thus there is no relative increase of lice on the outer aspect with increasing density. The population of an infested shirt tends to be distributed as follows (last columns of Table 4):

Inside: approximately a quarter of the total on each of the three areas—shoulder seams, side seams, general surface, with the remaining quarter divided more or less evenly between the remaining areas.

Outside: half of the population on the general surface, the other half distributed more or less evenly over the remaining areas.

Thus the proportions of the population on the seam areas and general surface areas differ for the two aspects of the shirt. These two main classes of habitat differ also, even for the same aspect, in the age distribution of the lice (Table 5). By seam areas are meant side seams, armpits, sleeve seams, neckband, breast and shoulders. 'General surface' areas include the main general surface and the general surface of the sleeve.

The analysis shows that approximately two-thirds of the total shirt population is in the seam areas; this general figure, however, bears little relation to the actual distribution when each shirt aspect and age group is considered separately.

With regard to the four main parts of the general surface (Table 4), the age distribution is more or less normal on both halves of the inner back surface but varies on the inner front surface from a very high larval proportion on the top half to a very high adult proportion on the lower half. As shown earlier, an unusually high proportion of these adults are males.

The effect of population density on the distribution in different habitats is illustrated in Fig. 2. The distribution curves may be divided into three phases, which correspond with the main phases of the frequency curve of distribution (Fig. 1), the first phase to the first mode, the second to the second and third modes, while the third corresponds to extreme densities (200 and over). In phase 1 the 'general surface' population is proportionately high at first (compare day 1 of Fig. 6). This suggests that many of the 1–10 density cases are instances of commencing reinfestation, where the shirt population is not in balance with the 'clothes-reservoir' population. In phase 2, the average values given in Table 4 are fairly consistently held, but in phase 3 the relative distribution is again upset.

Distribution on successive surfaces of two under-garments

Table 6 gives the distribution on the successive aspects, from within outwards (inside + outside of undervest, inside + outside of shirt) of all cases where a sleeved undervest and shirt were worn. The cases have been grouped according to the total population of the two garments. The lower part of the table gives the counts expressed in relation to a standard count of 100 on the inner aspect of the inner garment.

Over all densities the approximate distribution is: half of the lice are on the inner territory area, most of the remainder in the second territory area, and only a relatively small number on the outside of the outer shirt.

The age ratios are, in approximate figures, 1 : 4, 1 : $2\frac{1}{2}$, 1 : $1\frac{1}{2}$. In the individual groups the ratios, at least for the first and second territory areas, agree fairly well with this average at densities over 10, except for one aberrant ratio. At densities from 1 to 10, however, there is a relative preponderance of adults. This again suggests that such cases are often in the early stages of reinfestation, i.e. that many subjects have low counts because of a recent change of under-clothes, rather than because of their potential level being below 10.

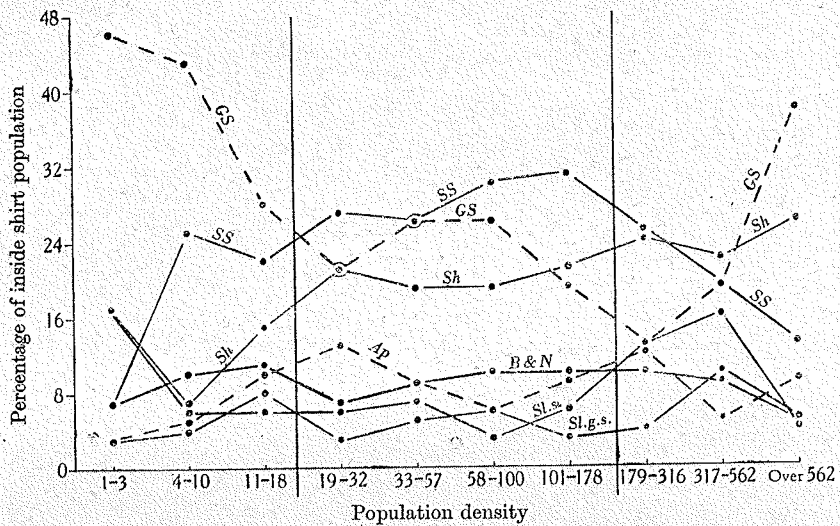

Fig. 2. Percentage distribution of lice on the different areas of the inside of the shirt at different densities. The three phases in the relation of the curves to each other are indicated by upright lines. In phase 2 (normal infestations) approximately one-quarter of the population inhabits each of three principal areas; at lower densities the relation is upset, indicating that many such populations are not in equilibrium.

Distribution on pants

Of the subjects examined who were wearing pants, in only 16 cases were the observations made sufficiently detailed to be of value. Of these, in 8 cases, a shirt, undervest and pants were worn, and in 8 cases, a shirt and pants. The comparative infestations, expressed as the totals inside + outside, were:

	Pants	Vest	Shirt
Adults/larvae	31/55 + 10/12	14/86 + 20/14	16/49 + 10/11
Adults/larvae	50/33 + 9/0	—	44/152 + 12/33

The summed totals for the 16 pairs of pants are 81/88 + 19/12, age ratios inside and outside of 1 : 1 and $1\frac{1}{2}$: 1, i.e. the pants appear to be comparable, in respect of age distribution, to the outer of two under-garments.

Table 6

Class interval	No. of cases	Adult/larval counts				Total	Counts per territory area			Age ratio for 1st and 2nd territory area		
1–5	11	8/8	+ 1/5	4/7	+ 1/0	34	8/8	5/12	1/0	1 : 1	1 : 2	
6–10	8	8/12	+ 6/11	5/7	+ 8/1	58	8/12	11/18	8/1	1 : 1½	1 : 1½	
11–20	5	6/24	+ 3/14	8/11	+ 3/11	80	6/24	11/25	3/11	1 : 4	1 : 2	
21–50	9	29/154	+ 12/37	5/33	+ 5/15	290	29/154	17/70	5/15	1 : 5	1 : 4	
Over 50	3	19/99	+ 23/36	13/43	+ 6/3	242	19/99	36/79	6/3	1 : 5	1 : 2	
Total	36	70/297	+ 45/103	35/101	+ 23/30	704	70/297	80/204	23/30	1 : 4¼	1 : 2½	1 : 1½
1–5		100	38	68	6							
6–10		100	83	60	43							
11–20		100	55	63	45							
21–50		100	27	21	11							
Over 50		100	50	47	8							
Total		100	43	37	15							

Table 7

Habitat	Inside	Outside	Ratio inside/outside	Age ratio inside surface
Waistband	14/19	2/1	11 : 1	1 : 1½
Crutch	17/34	6/8	4 : 1	1 : 2
General surface	26/23	4/1	10 : 1	1 : 1
Leg seams	7/10	0/0}	4 : 1	1 : 1½
Leg general surfaces	17/2	7/2}		8 : 1
Total	81/88	19/12	5½ : 1	1 : 1

Table 7 gives the distribution of adults and larvae in habitat areas. 'Waistband' includes the front opening; 'crutch' includes the central back seam up to the waistband; the 'general surface' excludes the legs.

Two points of interest are brought out in the table. The ratio inside/outside is markedly lower for the crutch than for the waistband and general surface. This suggests that the outside of the crutch is receiving lice from the fork of the trousers, and supports the suggestion of Peacock (1916) that the latter area is a focus of infestation.

On no part of the inner surface is there an age distribution comparable to that found in the breeding areas of the innermost territory area over the torso. The nearest approach to a 'breeding site' ratio is that of 1 : 2 on the inner crutch surface.

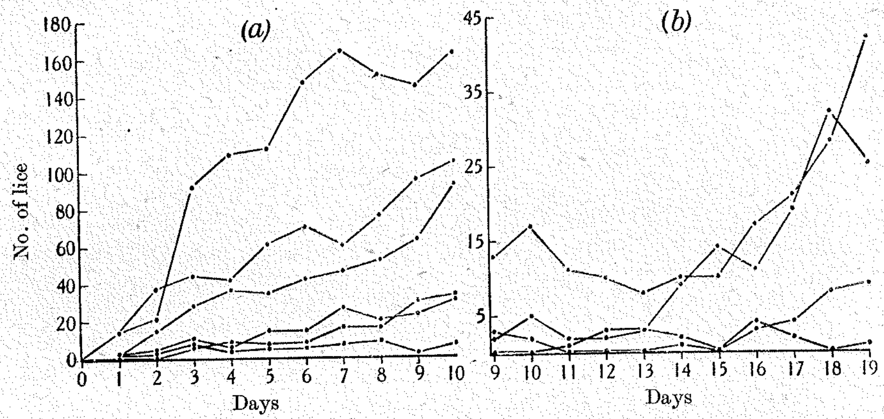

Fig. 3. (*a*) The individual curves for 6 men (group A) for the first 10 days after donning clean shirts, and (*b*) for four men from group C after partial delousement by 8 days' exposure to a pediculicide.

The infestation of clean shirts under verminous conditions

Twenty-one men, whose infestation levels were known from previous observations, were divided into three comparable groups each containing three men believed to belong to mode 1, three to mode 2 or 3, and one to mode 4. Each man was given a new army shirt, and instructed to wear it continuously against his skin. In the case of group B, the shirts were dressed, before issue, with a pediculicide, which continued to destroy practically all lice migrating on to them for the next 5–7 days. The group C shirts were similarly treated and retreated on the 8th and 16th days, so that they remained continuously unfavourable to lice up to at least the 20th day. Details of this work are given in another paper (Craufurd-Benson & MacLeod, MSS.).

The history of infestation of group A indicates what happens when a fairly representative group of men, habituated to a lousy environment, change their under-clothing. The individual curves, with one exception which will be discussed later, are illustrated in Fig. 3*a*. They show the range of variation resulting from the interplay of the two variables, reservoir pressure of population, and degree of inherent susceptibility, the environment being assumed to be constant.

The infestations in group C, after the 20th day, indicate the effect of the environmental contribution alone, since the clothes reservoirs have been exhausted by the unfavourable period of 20 days. Although some residual effect of the pediculicide will be present from 8 to 12 days after application, this is common to all the men, so that their relative rates of infestation are a measure of possible individual variation in response to a given environment. On the 28th day, 12 days after the last treatment, the infestations were 1, 1, 1, 0, 2, 2, 1, i.e. the rate of invasion was practically uniform.

The group B men, dressed only once, may be regarded as partially deloused men. Observations were continued on four of them for 19 days (Fig. 3*b*). If oviposition became possible by the 8th day, the second generation should begin to appear from the 17th day onwards. The sudden rise of two of the curves about the 16th day is probably due to this cause, i.e. up to the 16th day the infestations were due either to immigration from the clothes or invasion from the outer environment. Their comparative uniformity shows that, where the part played by the clothes reservoir in reinfestation is reduced, relative to that of the environment, the range of variation in individual infestation rates is also reduced.

Insusceptibility

If a man is exposed to the risk of infestation but remains free of lice it is at least possible that he is unattractive to lice, or an unsuitable host. An example is case 80 (subject 1 of group A), who had changed his shirt two days previous to the first examination. His louse count was 1/3+2/0 (inner and outer surfaces of shirt). This low count was attributed to the recent change of clothing, and a week later he was used for experiment. He was given a clean untreated shirt which he wore against his skin, without washing or changing, for 10 days. His daily counts, expressed as adult/larvae inside and outside, were:

Day...	1	2	3	4	5
	2/0+0/0	0/3+0/0	1/7+0/0	1/2+1/1	2/2+1/1
Day...	6	7	8	9	10
	2/4+0/0	2/3+1/1	4/2+1/1	2/0+0/0	6/1+0/0

There is here evidence of continuous infestation, but obvious failure of larvae (cf. 3rd to 4th and 8th to 9th days) or adults (cf. 1st to 2nd and 8th to 9th days) to establish themselves.

Other suggestive evidence of actual insusceptibility was obtained in a few cases, viz.:

Case 47/76. Among a group of men, examined on the same day, in a search for suitable material for experiment, four, all from common lodging house A, gave a history of having changed their under-garments within the previous two days. Their louse counts were all low, and they were rejected. Three days later these men were re-examined with the following result:

Case no.	1st examination	2nd examination	Increase
46	0/1+0/0	4/4 +0/2	9
47	0/1+1/0	0/2 +0/0	0
49	1/3+0/0	5/15+1/1	18
50	1/3+1/0	5/2 +2/0	4

(Counts expressed as adults/larvae, inside + outside of shirt.)

Case 47 was re-examined 26 days later (case 76). He reported that he had not changed his under-clothing since he was last examined, yet his count was 2/1+0/1.

Case 159. From a low-class Salvation Army hostel. History—shirt not changed for about 10 days previously.

Louse counts: undervest, 0/0+1/4; shirt, 0/0+0/1; i.e. few lice and none on the inner aspects.

Case 125 (Negro). From common lodging house A. History—shirt and undervest worn about a week (the vest was fleecy-lined and peculiarly suitable for lice). The count was: vest, 0/0+1/0; shirt, 1/5+3/7; i.e. greater numbers on the outer than on the inner aspects —a reversal of the usual order.

Apart from these four cases, no evidence of insusceptibility was obtained and it is believed that the phenomenon is uncommon. Hase (1915) includes insusceptibility in his four categories of individual reaction to infestation, but does not state the probability of its occurrence.

The development of an infestation

The development of infestation on the shirts of six of the seven men in group A is shown in Fig. 4*a*.

The total adult/larval counts for each day, are:

Day...	1	2	3	4	5
Total	21/10	26/56	41/148	40/168	42/194
Ratio	2 : 1	1 : 2	1 : 3·5	1 : 4	1 : 5
Day...	6	7	8	9	10
Total	56/235	64/257	62/262	100/258	130/299
Ratio	1 : 4·5	1 : 4	1 : 4	1 : 2·5	1 : 2

Thus, after 3 days of rapid increase, a primary balance is established between the outer clothing and the shirt; the numbers, particularly of larvae, then increase more slowly up to the 9th day. The adult/larval ratio also remains fairly constant from the 4th to the 8th day. On the 9th it is upset, probably by commencement of moulting of those larvae which had first migrated to the shirt, as recently hatched larvae, 7 or 8 days before. The rapid increase of adults is maintained on the 10th day, but the ratio is not correspondingly altered because a compensating increase of larvae has now commenced, resulting from the eggs of the earliest colonist females. The first of a 'native' population born on the garment in question, has now begun to appear.

Fig. 4*b* depicts the daily infestation of one subject from the group (case 81), who was known to have a low reservoir population, three counts over the previous month having given values of 14, 0 and 3. The infestation, up to the

9th day, is composed of relatively more adults than is the average for the group infestation, and illustrates the increased significance of the 'invasion increment' in building a shirt infestation, where the clothes reservoir is of low density.

Both graphs demonstrate the ebb and flow of lice from one aspect of the shirt to the other, obscuring the consistency of the increase in infestation.

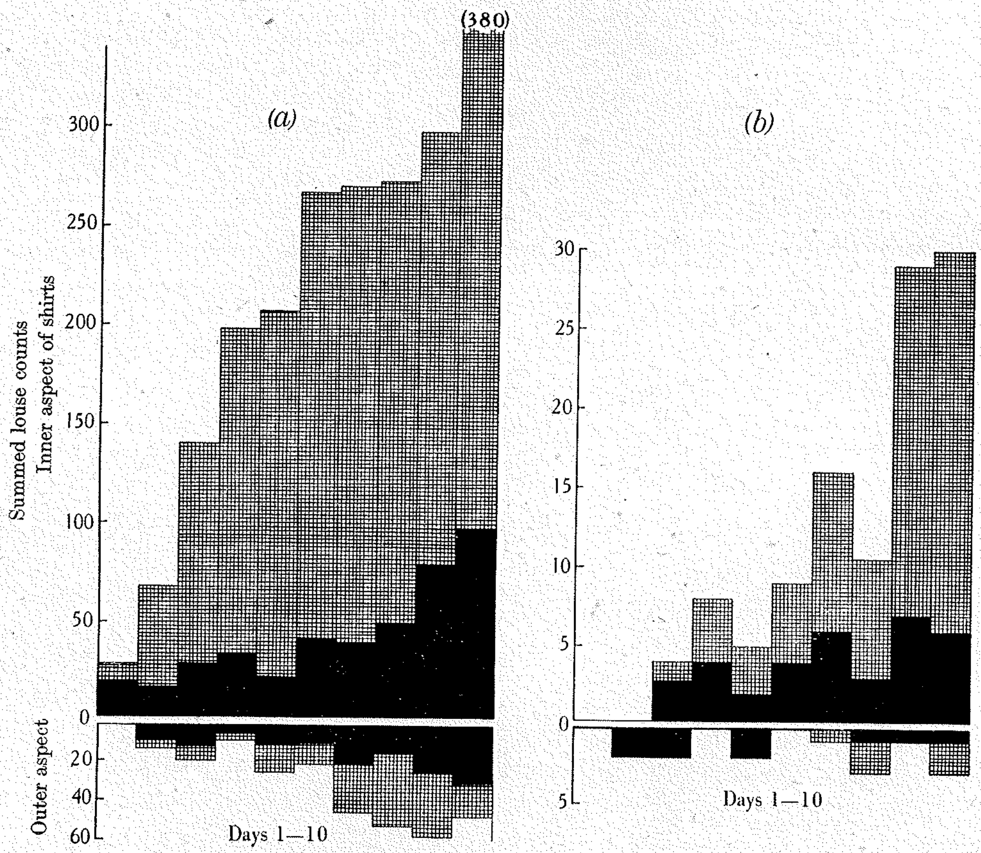

Fig. 4. (*a*) The daily total infestation of the shirts of six men from group A. The lower part of the diagram refers to the outside of the shirt. Black shading equals adults, interrupted shading, larvae. (*b*) The daily infestation for one of the six men, known to be lightly infested. Note the relative preponderance of adults, until the appearance of second generation lice on the 9th day.

Colonization of different habitat areas

Fig. 5 illustrates the progressive colonization of the different areas of the shirt, based on the total louse counts for the six men in group A. The infestation for the first 2 days, and each subsequent alternate day, is illustrated; the daily totals are given in Table 8.

The figure illustrates the following general trends in the process of colonization:

Day 1. Colonists mostly adults. General surface invaded.

Day 2. Migration to seams, larvae congregating there, and on shoulder areas. Adults present on outer aspect, probably migrating inwards.

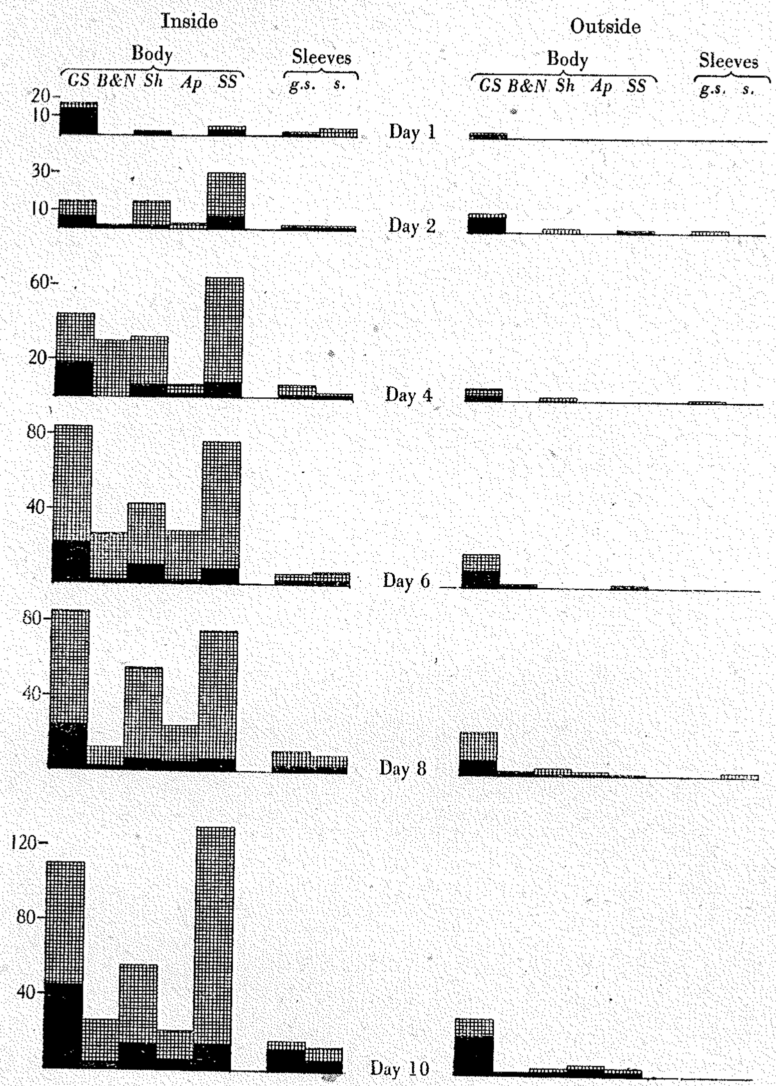

Fig. 5. The development of infestation of clean shirts, according to areas. The first 2 days, and each subsequent alternate day, has been figured. Black shading represents adults, interrupted shading, larvae.

Day 4. Larvae in the seams markedly more numerous. More numerous on the breast, neck and shoulder regions than on the general surface, suggesting that the path of migration to the inside is from above rather than from the trousers. General surface still principally populated by adults, who have presumably not yet reached the egg-laying sites—the seams.

Table 8. *Louse counts expressed as males/females/larvae.*

Day	*GS* Inside	*GS* Outside	*B+Nb* Inside	*B+Nb* Outside	*Sh* Inside	*Sh* Outside	*Ap* Inside	*Ap* Outside	*SS* Inside	*SS* Outside	*Sl.gs.* Inside	*Sl.gs.* Outside	*Sl.s.* Inside	*Sl.s.* Outside	Total Inside	Total Outside
1	7/8/2	0/1/1	—	—	0/1/0	—	—	—	0/3/2	—	0/1/1	—	0/0/4	—	7/13/9	+ 0/1/1
2	6/1/8	6/2/2	0/0/1	—	0/1/14	0/0/1	0/0/3	—	2/5/23	1/0/0	0/1/1	0/0/2	0/1/1	—	8/9/51	+ 7/2/5
3	7/6/15	5/4/3	0/0/19	0/0/1	2/4/28	1/1/2	1/0/6	—	1/5/71	0/0/1	1/0/0	0/2/0	1/0/2	—	13/15/141	+ 6/7/7
4	13/4/27	2/1/4	1/0/29	—	2/5/25	0/1/1	0/0/7	—	1/7/67	—	0/1/6	1/0/0	0/1/2	—	17/18/163	+ 3/2/5
5	6/6/39	5/5/7	0/0/25	0/1/0	2/2/25	—	0/0/21	1/0/0	4/4/67	0/1/1	1/0/2	2/2/1	0/0/6	—	13/12/185	+ 8/9/9
6	13/9/61	5/4/9	1/1/25	0/0/2	4/6/33	—	1/0/27	—	3/4/68	0/2/0	2/1/3	—	0/0/7	—	24/21/224	+ 5/6/11
7	12/8/96	10/5/17	0/3/12	0/0/2	4/6/45	0/0/3	1/0/15	1/1/2	0/6/57	1/3/0	0/1/2	0/0/1	0/1/5	—	17/25/232	+ 12/9/25
8	15/9/61	3/6/14	2/0/10	1/1/0	0/6/49	1/0/3	1/4/19	0/1/1	3/3/70	0/0/1	3/0/8	—	0/3/6	0/0/2	24/25/223	+ 5/8/21
9	18/19/58	7/12/26	0/3/18	1/0/1	10/6/55	0/1/0	3/2/16	0/1/1	4/3/57	1/0/7	2/0/8	0/0/1	2/5/10	—	39/38/222	+ 9/14/36
10	27/18/65	14/7/9	2/2/22	1/0/0	6/8/42	1/0/4	1/5/12	3/2/1	2/12/130	2/1/2	4/8/4	—	4/1/8	—	46/54/283	+ 21/10/16

Day 6. Population of armpits and shoulders increased. An increase of the general surface population, principally of larvae; this is reflected in an increase of the numbers of lice on the outside general surface, probably an 'overflow' effect.

Day 8. A slight increase on the shoulders and sleeves, but no marked change from the 6th, or indeed from the 5th day position (Table 8).

Day 10. Advent of 'native' lice. The seam concentrations of larvae have increased by hatching, and there has been generally an explosive increase of adults by moulting, resulting in an 'overflow' increase of adults on the outer surface.

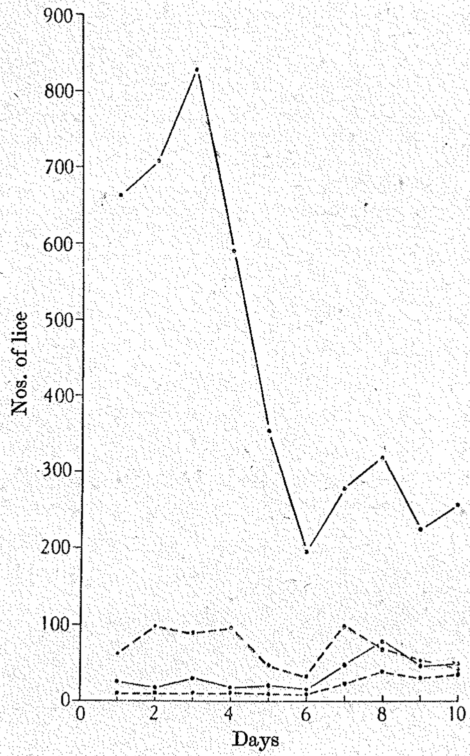

Fig. 6. The daily counts for the shirt of one excessively lousy subject in group A. The whole lines indicate the count on the inner surface, the interrupted lines that on the outer surface. The upper line of each pair refers to larvae, the lower to adults.

Observations on exceptionally heavy infestations

The seventh man of group A (case 86) was an exceptionally verminous subject. In one day his shirt count rose to over 700, and was almost 1000 by the 3rd day. This heavy infestation consisted of an abnormally high proportion of larvae, mostly 1st and 2nd instar, on the inner shirt surface. After a catastrophic decrease (Fig. 6) the population again steadied at a new level. Corresponding to this change, the adult/larval ratios on the two aspects changed markedly, the outer ratio approximating to the normal of 1 : 1 or 1 : 2, while the inner steadied at an unusually low larval proportion of 1 : 3–1 : 3½, as compared with the normal ratio of about 1 : 5.

Two infestations exceeding 1000 were recorded. The ratios in these were:

Case 74. Sleeveless vest and shirt. Total count 2600. Adult/larval ratios: undervest, $1:4\frac{1}{2}$, $1:1\frac{1}{2}$; shirt, $1:1\frac{1}{3}$, $1:1$.

Case 114. Two shirts and no vest. Total count 1217. Ratios: inner shirt, $1:4$, $1\frac{1}{2}:1$; outer, $2:1$, $8:1$.

In the second case the larval ratio is unmistakably abnormal, with a marked adult preponderance on all surfaces but the innermost, and it is at least possible that this population had recently suffered a severe reduction of its larvae, similar to that observed in case 86 (Fig. 6).

Three other instances of relatively high infestation (500–1000) were obtained. In all three the subjects wore a shirt against the skin. Case 257, with a total population on the shirt of 866, showed inside and outside ratios of $1:74$ and $1:9$ (compare days 1–3, Fig. 6). Case 186, shirt population 862, showed the approximately normal ratios of $1:5$ and $1:2\frac{1}{2}$. Case 29, shirt population 518, showed ratios of $1:2\frac{1}{2}$ and $1:1$.

These figures might be interpreted as indicating that the infestation in case 257 was building up to an unbalanced climax preceding a collapse, that of case 29 had just 'crashed' through disappearance of larvae, while case 186 apparently still possessed a balanced, or stable, population.

At lower densities sudden changes of the level of a shirt population have been observed, but these could usually be related to some physical factor. Thus, in men under regular observation it was noticed that if on arrival their shirts were damp with perspiration, the damp areas were invariably deserted by the lice, the total count being sometimes much reduced. Such fluctuations were usually redressed by the following day. With senile subjects, where the lower part of the shirt was often soiled with urine, the lice were similarly found to forsake areas such as the lower side seams, when these were wet, but the armpit and shoulder counts in such cases were often correspondingly increased.

Résumé

From a study of natural infestations of over 200 sets of under-garments, the following conclusions seem permissible, at least as provisional working hypotheses.

Under-garment infestations tend to fall into four groups: those with totals of under 10 lice, between 30 and 60, 100 and 150, and those of over 200 lice.

Individual subjects tend to remain in a given infestation group.

The number of under-garments worn by a subject does not influence his infestation level.

Except at extremes, under-garment populations show certain characteristics which allow the 'normality' of the population to be judged. (An infestation is held to be 'normal' when the proportion of lice on the under-garments to those on the outer clothing is in equilibrium, so that alteration of the numbers on, say, the shirt occurs only as a result of alteration of the subject's total infestation.) The 'normal' characteristics are: (*a*) the relative distribution of the population in the different areas of a garment (see next paragraph), (*b*) the proportion of the population on the inner and outer aspects, this ratio remaining fairly constant irre-

spective of density, and (c) the proportion of adults to larvae on the different aspects, which is fairly constant for densities between 10 and 500.

The habitat distribution on the inner surface for 'mode 2' and 'mode 3' infestations is constant. Modes 1 and 4 infestations show irregularities, but their normality may, however, be judged by the age ratio and the distribution between the different aspects or territory areas.

An under-garment population of low density because of a recent change of under-garments will naturally not be in balance with the sources from which it arises; it is recognizable because of (a) the abnormal habitat distribution, too high a proportion being on the general surface, (b) the abnormally high adult proportion, approximating to 1 : 1 or 1 : 2, and (c) the abnormal distribution between the inner and outer aspect, or between the first two territory areas, relatively too many lice being in the outer territory. At very high levels of density, the population may be unbalanced because of violent fluctuations from unknown cause, expressed principally by alteration of the larval population level. Such a population is recognisable before or after a decimating fluctuation by the excessively high or excessively low larval proportion respectively.

From a study of the process of colonization of clean shirts issued to infested subjects, the following points emerged.

The shirt infestation appeared to come into equilibrium with the total population in 3–6 days, after which the population rose slowly until the 9th day, when 'native' lice began to appear, and the primary infestation equilibrium was upset.

The rate of infestation and primary equilibrium level differed markedly from man to man, although they all lived in the same common lodging house. When a similar group was deloused so that the rate of infestation of the shirt was due solely to the invasion increment, little variation was evident in their individual infestation rates. In insusceptible cases, lice failed to establish, so that the subject's infestation at any given time represented little more than the invasion increment for that moment.

During the first day or two after donning of a clean shirt, both the relative distribution in different habitats and the age ratio were abnormal. Similar aberrations were found in natural infestations with a population density below 10, and it is probable that many of these are instances of active reinfestation.

Discussion

The population of the average cheap hostel is by no means predominantly vagrant in character, all grades of working-class men being represented. The observations made should not, therefore, be regarded as a study of lousiness among a class who accept lousiness as natural, but as an indication of what happens when men of all classes are grouped together under conditions which allow of vermin surviving, as for instance in refugee camps or in an army on active service.

In a verminous environment freedom from casual infestation by contact or otherwise, is ordinarily impossible. On the other hand, a verminous environment is obviously not essential to the continuance of an infestation. As a third generalization it may be stated that, in a body of men living in the same environment, wide variations occur in the degree of infestation. The respective parts played by the environment and the man in developing and maintaining an infestation thus invite consideration, and some information has been obtained on this subject from a study of the infestation of clean shirts worn by deloused, partially deloused and lousy men.

It has been shown that the rate of reinfestation of clean garments is predominantly influenced by the immigration rate from the outer clothing, which varies with the pressure of the population reservoir there. When this source of reinfestation is removed, there is seen to be a basal invasion rate from outside sources, which is fairly uniform over a given group, its value depending on the environment and not on the individual.

In a group of men newly introduced to a verminous environment, the initial infestation should therefore be fairly equal. The fate of the invading lice will, except in cases of insusceptibility, depend on the degree of personal care exercised by each man, so that, after a period, 'outer clothes populations' of varying density are built up in the same group. The chief factor influencing density will usually be the frequency of change of under-garments.

Once the 'clothes reservoirs' are established, the immigration rate on to clean under-garments will vary widely within the group, men with a high clothes reservoir being penalized by more rapid reinfestation. Differences are thus accentuated, so that after a time it should be possible to divide a group exposed to a uniform environment into subgroups of different degrees of lousiness according to the frequency with which they change their under-garments.

Now, the intervals between changes of under-garments are generally divisible into four or more categories: daily or two daily, with men of clean habits, weekly in a very large proportion of men, each alternate week among some men, many of whom have the habit of changing only the outer of two under-garments weekly, and at prolonged and irregular intervals, in careless or very destitute sections of a population. The frequency distribution of infestation tends similarly to show grouping about different density levels, and it is suggested that the two are causally related.

The position may be summed up by saying that infested individuals very soon become victims of their own habits, rather than of their environment, in so far as their louse burdens are concerned. This is well illustrated in Fig. 3*a* (group A men). Although the men in question were exposed to a more or less uniform environment (excluding their beds, which can here be classed with their outer clothing), the shirt infestation levelled out at an equilibrium characteristic of each man. In one respect, however, these men were divorced from their normal routine—they were all obliged to wear the same shirts, unchanged, for the duration of the experiment. Except in the case of one insusceptible man, the light and medium infestations began to increase as a result of the appearance of native lice, indicating that the control of louse populations at different levels is due, not to peculiarities inherent in the subjects, but to their habits, and is upset where the habits are changed.

In control experiments with naturally infested subjects, the post-treatment counts must obviously be regarded in relation to those before treatment. It is essential, to avoid misinterpretation, that the pretreatment counts be representative of the men's 'normal' infestations. A man chosen at random may have a high potential shirt infestation, but may have changed his shirt, say, the day before examination; his count will be fictitiously low, and treatment appear unduly ineffective. It is suggested that, by the criteria of normality developed above, this source of error may be obviated, if age—and regional—distribution are noted at the first count.

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