INTRODUCTORY REMARKS

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Before discussing the bionomics of human lice, it seems desirable to assess the relative hygienic importance of body lice, head lice, and crab lice. While all of them are disgusting and irritating parasites, their potential as disease vectors is more serious and is presumably the main reason for this Symposium. The body louse has generally been regarded as the usual agent, (*1*, *6*) though it was long ago claimed that head lice can also transmit typhus (*20*) and more recently it has been demonstrated that the rickettsiae can proliferate in both head lice and crab lice (*24*). Also, the spirochetes of relapsing fever can apparently reproduce in both head and body lice (*19*). These laboratory data do not, of course, prove the vector status of lice in the field, which is likely to depend as much on their behavior as on their receptivity to pathogens.

Habits, habitats, and vector capacity

It is convenient to dispose first of the crab louse *Pthirus pubis*, which apparently has the lowest vectorial capacity. From the two studies of its biology available (both made over 50 years ago), it is evidently quite dependent on man. Of 200 specimens removed from a man and kept in favorable conditions, only one was alive 24 hours later (*21*). It is also very sluggish, with a maximum range of about 15 cm (*21*, *23*). It is true that crab louse infestations are liable to spread slowly through a group of men living closely together (e.g., ship's crews or soldiers in the field) (*9*), but it seems unlikely that this insect could initiate or maintain a disease epidemic.

The unimportance of the head louse is less certain. It is very closely related to the body louse in that, though they generally differ on several anatomic points, these overlap, so that none is categorical (Figures 1 and 2); and they will interbreed freely, though the prevalence of hermaphrodites in the progeny suggests a certain incompatibility (*16*). Some 50 years ago, Nuttall (*22*) thought the two forms were merely "unstable races of one species," basing his belief largely on the fact that a head louse colony maintained by A. Bacot in pill boxes on the body had seemed to change into typical body lice, over a period of two to three years (*16*). Ferris (*10*) withholds judgment, however, recommending ". . . extensive experimental work to carry further the investigation of the problem which has been set." When I attempted this, I found that colonies of the two forms remain distinct when reared under identical conditions for about 40 generations (*4*), so that genotypic differences must be involved, and it seems reasonable to regard them as subspecies (*Pediculus humanus humanus* and

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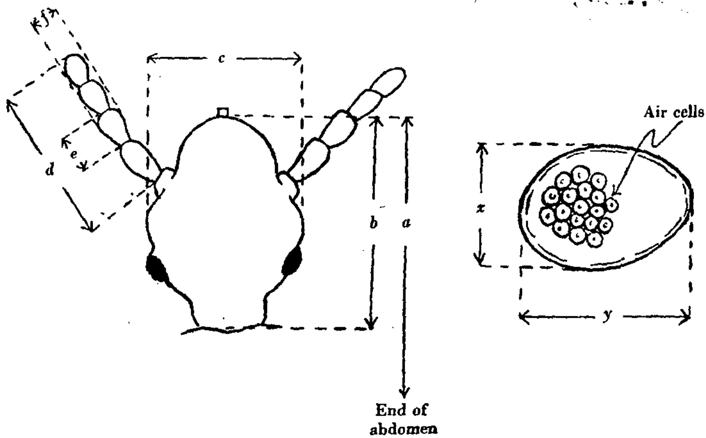

Figure 1. Measurements used for comparing body lice and head lice. After Busvine (4).

P. h. capitis). It is very probable that the head louse was the ancestral type and that the body louse evolved from it as we began to wear clothes. Clothing constitutes a more rigorous habitat than scalp hair since clothes move about when the host is active and can be removed completely; in both cases, opportunities for feeding are restricted. This may be the reason why the body louse form is larger, more resistant to starvation, and more adaptable to rearing in captivity.

Though body lice tend to be most common on the undergarments next to the skin, they wander about extensively, as I found in some simple tests about 30 years ago (*3*). Lice put onto the center of the back of a man's vest, or undershirt, wandered an average of 30.5 to 35.5 cm within two hours. Other experiments showed that exercise which produced sweating increased their restlessness. In heavy infestation, lice emerge on the upper clothes and are fairly easily transferred in crowds. Mackenzie, writing of severe typhus epidemics at the end of World War I, remarked, " . . . men visiting markets to buy food for our Units, almost invariably returned with one or two lice on them" (*17*).

Evidence about actual transmission of head lice is scanty, though they are known to spread among children at school. Apart from this, they are commonly regarded as passing round members of a family.

In civilized communities, the habit of living mainly on clothing has restricted body lice to a small minority of socially inadequate people who seldom wash or change their clothes. Head lice, however, are still regrettably prevalent, mainly in children (especially girls) who may be otherwise quite clean. It is difficult to believe that this represents any potential threat of louse-borne diseases though some very early records of endemic typhus in the Philippines, in 1915, suggest that head lice were responsible (*12*). There do not, however, seem to be records of any epidemic of louse-borne disease when body lice were not common. On the other hand, simultaneous infestations with both

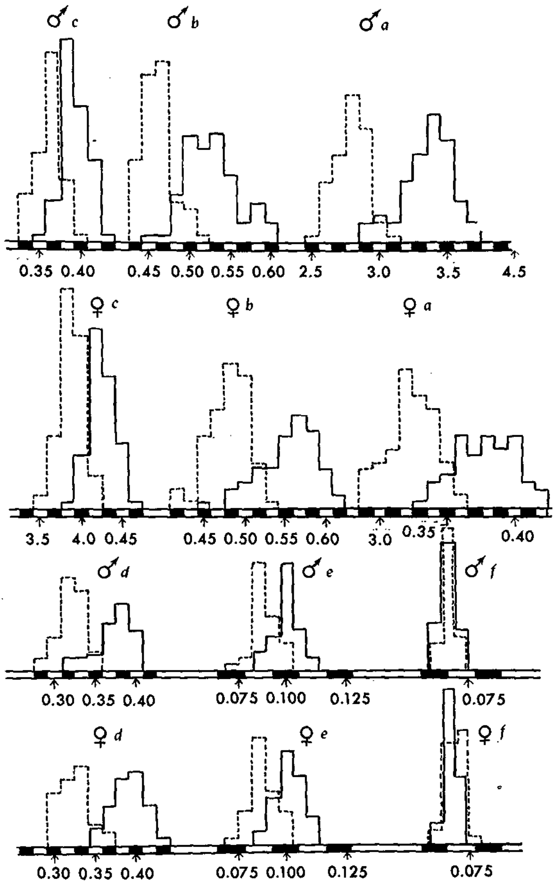

Figure 2. Histograms showing distribution of sizes of various dimensions of head and body strains of lice. a = total body length; b = length of head; c = width of head; d = length of distal four segments of antenna; e = length of third antennal joint; f = width of third antennal joint. Solid line represents body lice and dotted line represents head lice. After Busvine (4).

forms were observed among poor people in Poland at the time of World War I. Hase (*14*) examined 1,000 of them and found the results shown in Table 1:

Table 1. Number of lice found on 1,000 poor people in Poland during World War I.[a]

	Body lice	Head lice	Both forms
Men	50	29	29
Women	90	55	35
Children	73	60	13

[a] From: A. Hase (*14*).

Bionomics of Pediculus humanus

The earliest scientific studies of louse biology were made on small colonies maintained in pill boxes kept, more or less constantly, on the human body. Many of these investigations are summarized in Buxton's book (*6*). Somewhat later, I made an even more comprehensive study, also involving a head louse colony. The results (Table 2) show the very similar development rate of the two subspecies. In other respects, the body louse is more efficient, in its lower mortality during development, its longer survival, and greater egg-laying capacity.

Colonies reared in pill boxes are inconveniently small for screening trials of insecticides and, about 1946, mass-rearing methods were developed in the United States. At first, these still depended on human blood meals, lice kept on felt pads in incubators being fed daily on paid donors. Rearing, under these conditions, took nine to 11 days and the adults lived 22 or 23 days. Females laid about 4.5 eggs per day, of which 85 to 95 per cent hatched in eight or nine days (*7*).

A remarkable advance was then achieved by adapting human louse colonies to feeding on rabbits (*8*). These animals differed considerably in suitability as hosts, only seven of 97 tested being found favorable. The longevity and fecundity of lice reared on the favorable rabbits were not markedly inferior to those reared on man, however.

In the mid-1960's, the results of two bionomic studies of lice reared on rabbit blood appeared. Gooding (*13*) investigated the effects of frequency of feeding, by allowing the nymphs meals at various intervals, ranging from four to 48 hours, and the adults at intervals from 12 to 96 hours. He claimed that the results (Table 3) fitted two unusual formulae:

$$f = \frac{k}{(\log t)^a} \text{ and } ft = \frac{kt}{(\log t)^a}$$

where f = number of meals, and t = interval between meals, while k and a were constants. This formula was intended to allow for an "optimum" feeding interval, conceivably indicated by the slightly deleterious effects of the four-hour period. But since the averages quoted depend on only two replicates of 10 lice (some of which died), it is doubtful whether this can be sustained. The data fit an approximately hyperbolic relationship between feeding interval and development. The two asymptotes would be shortest development (about 11 days) with maximum feeding and the shortest feeding interval (about 48 hours) which causes starvation (i.e., infinite development time). The adults show a similar benefit from more frequent feeding, at least to the shortest interval tested (12 hours).

Flemings and Ludwig (*11*) investigated the effects of temperature and parental age on the bionomics of rabbit-fed lice using two colonies, one susceptible and the other DDT-resistant (Table 4). The offspring of very young or very old lice showed no obvious change in rate of development or survival as adults. They did, indeed, lay fewer eggs per female-day, but the authors state that the differences were not significant. They appeared to find interactions in the factors tested (e.g., a different optimum temperature for strain combinations), but these seem somewhat unconvincing. Over the small

Table 2. Bionomics of head and body lice reared on human blood.[a] [b]

		Averages for							
		Head lice				Body lice			
Worn on body (hours/day)		24	12	2×3	3	24	12	2×3	3
Nymphal period	days	8.5	12	18	23	8.3	13	18	24
	% mort.	15	35	32	97	0	9	9	64
Adult life (days)	males	10	—	—	—	20	30	30	13
	females	9	22	17	—	20	21	25	15
Eggs	per female/day	6.3	2.5	1.3	—	5.5	4.7	2.9	1.0
	totals	57	56	22	—	110	98	75	15
	% hatch	88	76	64	—	94	91	78	0

[a] Lethal starvation of head lice is 55 hours and of body lice 85 hours at 23°C, and of head lice 24 hours and of body lice 45 hours at 30°C.
[b] From: Busvine (*4*).

range investigated, increased temperature has the expected effect of shortening development and adult life, but it increased oviposition so that a compromise seems to give the maximum egg production at the intermediate temperature.

Summary of bionomics. Optimum conditions for the louse would appear to combine temperature of the human skin (30° C) with continuous opportunity for feeding on human blood. Colonies adapted to feeding on rabbits show little effect on speed of development or the length of adult life, but the females tend to produce fewer eggs per day. With restricted feeding, a meal must be given at least daily. More frequent feeding has little effect on development, but improves egg production somewhat.

Table 3. Bionomics of lice reared on rabbits with various feeding intervals.[a]

Feeding interval (hours)	Nymphal period (days)	Mortality (%)	Adult female life (days)	Eggs/female/day	Hatch (%)
4	11.5	40	—	—	—
8	11.3	10	—	—	—
12	—	—	19.3	3.6	89
16	11.8	15	—	—	—
24	13.1	10	17.5	2.2	87
32	13.9	35	—	—	—
36	—	—	10.4	1.3	51
40	15.5	70	—	—	—
48	—	100	10.0	1.0	54
72	—	—	8.8	0.6	45
96	—	—	5.8	0.1	0

[a] From: Gooding (*13*).

Population growth

Buxton (*6*) makes some interesting calculations of expected population growth of body lice, based on their vital statistics, when reared under artificial conditions (on man, in pill boxes). Subsequent work might alter some of his data one way or the other, but not so far as to appreciably change his con-

Table 4. Bionomics of lice reared on rabbits and held at different temperatures.[a]

	Temperature (° C)	32.2	30.8	29.4
Days (av.)	Egg stage	6.0	6.7	8.5
	Nymphal stage	10.0	10.4	12.8
	Female life	14.5	15.1	17.6
	Male life	15.6	15.6	18.3
Eggs	Per female (day)	2.85	2.95	2.63
	% hatch	85.5	85	79
	Viable eggs/female	34.5	37.8	36.5

[a] From: Flemings and Ludwig (*11*).

clusions. He calculated that, under favorable conditions, the progeny of a single female would grow to between 4,000 and 5,000 in three months, and to between 400 and 500 if conditions were unfavorable.

If we now compare these estimates with actual numbers of body lice (or head lice) found on infested people, there is an obvious inconsistency. Even under very squalid conditions of general lousiness, the great majority of people carry small numbers, of the order of a dozen or so. Smaller numbers of infested people are found with populations up to several hundreds, while infestations of thousands are very rare indeed. Williams (*25*), who examined some of these data (for head lice, in tropical prisons), found that they fitted a logarithmic series proposed by the mathematician R. A. Fisher (in this, the numbers of people with 1, 2, 3, . . . lice is represented by $\frac{n}{1}, \frac{nx}{2}, \frac{nx^2}{3} \ldots$, where x is constant for a given series, always less than unity) (Figure 3).

If we return to the problem of the rarity of very heavy infestations, it is clear that some population check must exist. It is unlikely that this could be competition for food, which is virtually unlimited. (I calculate that 1,000 adult lice would only consume about 1 ml of blood per day.) Another important regulator of insect populations is also inoperative; that is, adverse climatic conditions. Lice living permanently close to the human body experience very favorable, equable conditions, which are largely independent of changes in the general climate. Thus, experiments in Iran (*18*) showed rather uniform temperatures under clothing (28°-32° C), despite wide variations in the external temperature in summer (34°-37°) or winter (16°-20° C). Analogous experiments in England (*4*) showed temperatures near the scalp to be 30°-33° C, either indoors at 18.5° or outdoors at 13° C.

Buxton (*6*) reviewed other causes of louse death, some of which are evident to those who have maintained colonies. A small number die with ruptured guts, so that the contents escape into the hemocoele; the cause is unknown. Some females seem to suffer occlusion of the oviduct perhaps owing to intrusion of the cement used to fasten eggs, and become enormously swollen and die. First-stage larvae often find difficulty in feeding, even on bare skin; this may be more prevalent on some people than others and also on the part of the body chosen for the first meal.

Lice are virtually unaffected by arthropod parasites or predators. A few infections by microorganisms are known; for instance, a bacillus that lives in the copulatory organ, a *Herpetomonas* in the gut, and a microsporidian. Certain rickettsiae harmful to man are also fatal to lice, though the spirochetes of relapsing fever do not seem to harm them. In general, there is little evidence of significant mortality from microorganisms, even in crowded colonies.

It appears, then, that the main population check is from the delousing operations of man. Buxton points out that these have two characteristics:

1. Man does not act regularly, killing a small proportion daily; on the contrary, he selects a particular day for washing his shirt or taking some sort of drastic action. The mortality that he produces is therefore exceedingly irregular.
2. On the whole, man's activity will be more intense as the population of lice rises, so that the mortality produced will tend to be a function of the density of population.

The second point must indeed be beneficial to lice in the early stages of transfer to a new human host, since the transfer must presumably involve only a few specimens and represent a vulnerable period. On the other hand, there is another difficulty that very small groups of lice are liable to encounter in founding a new colony: the propensity of

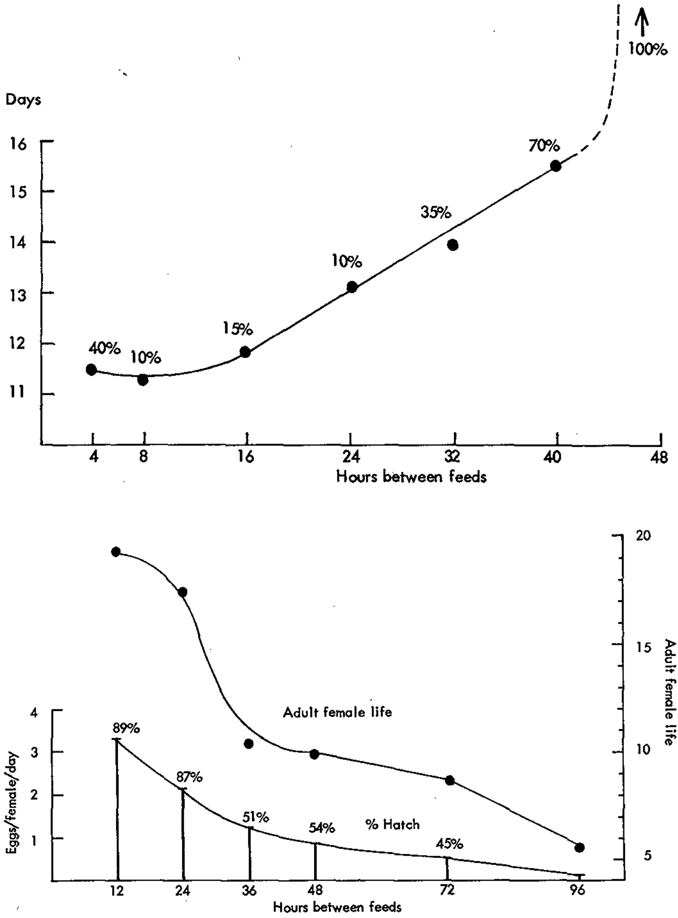

Figure 3. Bionomics of body lice reared on rabbits, with different intervals between feeds. Top: mean development period and mortality. Bottom: mean adult female life, egg production, and percentage of hatch. After Gooding (13).

the offspring of single pairs to consist very largely of individuals of one sex or the other. This has been observed by several workers; and though the cytology of oogenesis and spermatogenesis has been described by several workers, and has certain interesting features (*15*), no explanation for this has been found.

The practical consequences of obtaining progeny almost exclusively male can be imagined (and this tends to complicate genetic investigations with lice). The reverse condition is less serious, and since both abnormal ratios are about equally common, the sex ratio of a large colony or infestation is generally close to 50:50.

Biology away from the host

In the "normal" temperature range

From eons of close association with man, lice have become extremely dependent on his close proximity and, in contrast to many other blood-sucking arthropods, very soon die from starvation or temperatures a little removed from optimum. This is illustrated by the data in Figure 4, which also shows the narrow range within which eggs will hatch. From the combined data it is evident that infested clothing away from the host for a month could not possibly harbor living lice, even if long-surviving adults laid eggs just before dying. The period of complete ex-

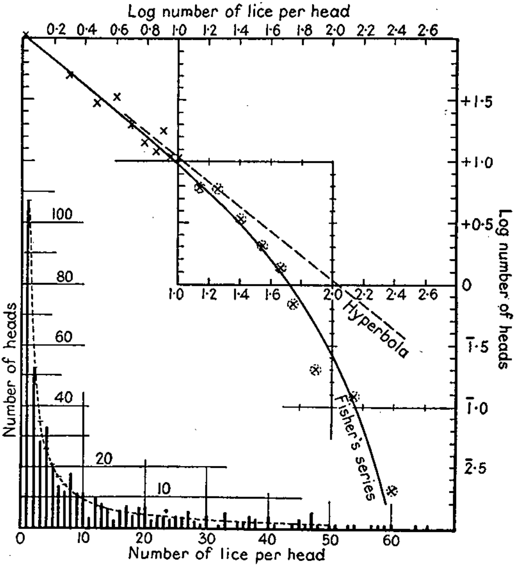

Figure 4. Number of lice on the heads of Hindu prisoners in Cannanore, India, jail (461 heads, 7,442 lice) are shown in lower part of figure. Attempt to fit these data, on a double logarithmic scale, to a hyperbola and to Fisher's logarithmic series is shown on upper part of figure. After Buxton (6).

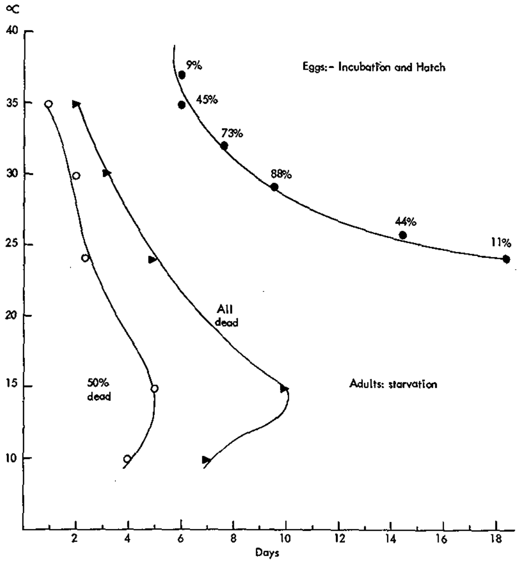

Figure 5. Effects of environmental temperature on incubation period and hatch percentage, and on survival of adults without food. Data from Buxton (6).

termination must normally be much shorter than this.

High temperatures

For short exposures to high temperature, the most resistant stage of the life cycle is the egg (Figure 5). But even eggs succumb after five minutes at 51.5° C or 30 minutes at 49.5° C (5). It is therefore quite possible to delouse clothing or blankets by immersion in hot water (as for 10 minutes at 60° C). This is, however, most inconvenient, since it demands facilities for drying the fabrics afterwards. The use of hot air presents the difficulty that the lice are mostly protected by layers of insulation. As a result, an exposure to still air at 70° C for an hour is necessary, though this period can be reduced by air circulation (2).

Low temperatures

Louse eggs are also the most tolerant stage for exposure to low temperature. A temperature — 20° C for five hours or of — 15° C for 10 hours is fatal (2). But even longer exposures or lower temperatures are necessary to kill louse eggs protected by insulation, which renders the method highly impractical for control purposes.

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