THE INFLUENCE OF NUTRITION ON EGG-PRODUCTION AND LONGEVITY IN UNMATED FEMALE BODY-LICE (*PEDICULUS HUMANUS CORPORIS*: ANOPLURA)

BY

A. J. HADDOW, M.B.

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THE INFLUENCE OF NUTRITION ON EGG-PRODUCTION AND LONGEVITY IN UNMATED FEMALE BODY-LICE (*PEDICULUS HUMANUS CORPORIS*: ANOPLURA)

By A. J. HADDOW, M.B.
London School of Hygiene and Tropical Medicine

(With 1 Figure in the Text)

Introduction

The object of the present experiment was to determine to what extent the longevity and yield of eggs of female body-lice is affected by the length of time allowed daily for feeding. The main difficulty has been to ensure uniformity of conditions and to make the feeding period, as far as possible, the only variable.

Bacot (1917) pointed out that female lice will lay eggs before fertilization and in the continued absence of males, though these infertile eggs do not hatch. His findings have been amply confirmed. Buxton (1937) has shown that the presence of males in large numbers may have a detrimental effect on females, decreasing both their reproductive activity and their longevity. This is apparently due to repeated copulation and to the injuries—sometimes fatal—which may be inflicted during this rather violent act. For these reasons it was decided that only unmated females would be used in the experiment. This provision also eliminates such possible influences on reproductive activity as early death of the male.

The lice were reared and kept in small pillboxes floored with bolting silk. These were worn under the sock as suggested by Buxton (1939). The insects were isolated in the last larval stage to prevent the possibility of fertilization, which may occur within the few hours following the last moult. To secure uniformity it was necessary to wear the lice continuously and on no occasion was a female removed from the body for more than 20 min. each day—the time required for washing and for counting the eggs. The day was divided into 4 hr. periods and groups of ten females were fed for 24, 20, 16, 12, 8 and 4 hr. per day respectively. Another group of ten was never fed after the last moult had taken place. To prevent feeding at other times, the boxes were placed, in the intervals, in slightly larger half-pillboxes. The floors of these were of double thickness and were perforated by several holes of 5 mm. diameter which allowed air to circulate between the skin and the interior of the box containing the louse. Thus the only essential difference between feeding period and interval was that during the latter the gauze floor of the box was raised sufficiently from the skin surface to prevent the louse biting. The feeding period was always a single unbroken stretch. The time at which it started was

varied a little from day to day in case some activity of the host, taking place at a fixed hour daily, might influence the lice. In no case was a batch made up of females which had emerged on the same day. This provided that, should a particular day prove unusually favourable or otherwise, its influence would not be brought to bear on all members of a group at the same period of life. The boxes were all worn under the socks but their positions were changed daily in case one area might be better than another. All the lice were fed throughout adult life on a single host—the writer—and the great majority were reared from the egg or first instar on the same host and under the same conditions as the adults.

Marsh & Buxton (1937) and Mellanby (1932) have demonstrated the striking uniformity of temperature and humidity existing between the clothes and the trunk under varying atmospheric conditions. The present experiment thus approaches controlled conditions, these unmated lice being confined singly throughout their adult life in identical boxes, always in communication with this very stable atmosphere next to the skin and always on the same host. The experiment took place during the very cold weather of December–January 1939–40 and in practice it was suspected that the temperature under the socks did fluctuate somewhat as, on one or two extremely cold days, the egg production of all groups was diminished.

The eggs were counted and removed daily, each louse being given a fresh piece of black tape for oviposition. Eggs were rarely laid on the box itself but were frequently deposited on the gauze. This was particularly common during the first few days of adult life in all groups and throughout life in the case of underfed groups.

The group of ten was found to be rather small, a single louse being able to sway the final results for the batch to some extent, but was necessitated by the fact that there is a limit to the number of lice which can be tolerated over a long period.

Results

General

The results for each louse are given in Table 1, the individuals of each group being arranged in order of longevity. Group totals, means and standard deviations are given in Table 2.

The normal pre-oviposition period was 1–2 days in all groups. In six individuals only (all from batches fed 12 hr. or over) was it prolonged to 3 days. The full rate of production is not attained till the fifth or sixth day. From this time on the rate is maintained till shortly before death. As a rule no eggs are laid on the last day of life but occasionally numbers up to four were recorded. In view of the statement made by Nuttall (1917) that high rates in comparison with previous figures might be attained if lice were worn continuously, it is interesting to note that in the 24 hr. group 200–300 eggs per louse was a common figure, 329 being the highest recorded. Very high rates of laying

Table 1. *Records of longevity, egg yield and rates of laying, of individual lice (a, b, etc.)*

Hours...	24			20			16			12			8			4		
Ref. no.	Days life	Eggs	Eggs/day	Days life	Eggs	Eggs/day	Days life	Eggs	Eggs/day	Days life	Eggs	Eggs/day	Days life	Eggs	Eggs/day	Days life	Eggs	Eggs/day
a	6	11	1·8	5	10	2·0	20	133	6·7	7	13	1·9	3	3	1·0	4	3	0·8
b	17	121	7·1	5	12	2·4	23	148	6·4	19	114	6·0	4	2	0·5	4	3	0·8
c	30	228	7·6	30	218	7·3	26	169	6·5	26	175	6·7	4	2	0·5	5	2	0·4
d	30	246	8·2	30	243	8·1	29	199	6·9	28	178	6·4	4	2	0·5	9	23	2·6
e	32	263	8·2	31	254	8·2	29	203	7·0	29	199	6·9	5	9	1·8	9	29	3·2
f	33	220	6·7	33	174	5·3	30	198	6·6	29	207	7·1	5	10	2·0	10	20	2·0
g	36	282	7·8	33	258	7·8	35	246	7·0	31	220	7·1	21	99	4·7	10	33	3·3
h	36	296	8·1	35	238	6·8	37	249	6·7	34	239	7·0	22	89	4·0	18	61	3·4
i	38	329	8·7	38	262	6·9	41	296	7·2	35	227	6·5	30	169	5·6	28	123	4·3
j	40	310	7·8	42	171	4·1	44	270	6·1	38	264	7·0	36	196	4·3	36	189	5·6

Table 2. *Group totals, means and standard deviations. The latter are calculated with a correction for small samples* (Hill, 1937, p. 46)

	Longevity (days)			Egg yield			Eggs/louse/day	
Hours	Total	Mean	S.D.	Total	Mean	S.D.	Mean	S.D.
24	298	29·8	10·4	2306	230·6	96·6	7·7	2·0
20	282	28·2	12·7	1840	184·0	96·3	6·5	2·3
16	314	31·4	7·7	2111	211·1	53·1	6·7	0·3
12	276	27·6	8·9	1836	183·6	72·4	6·7	1·6
8	134	13·4	12·6	581	58·1	75·1	4·3	3·7
4	133	13·3	10·8	486	48·6	60·0	3·7	1·7

were maintained for short periods by single lice—in the 24 hr. group it was quite common for a louse to lay ten eggs per day for 4 or 5 days in succession. Eleven eggs in a day was quite a common figure among members of the 12–24 hr. groups and the 20 and 24 hr. groups sometimes reached the figure of twelve. In the 24 hr. group 13 eggs were laid in 1 day on two occasions. It was noted, however, that except in the 20 and 24 hr. groups these very high figures are usually followed by a fall on the subsequent day. It appears probable that, for practical purposes, ten eggs per day is the highest rate that a louse can be expected to maintain. The highest rate recorded in the present experiment was 8·7 eggs per day for entire life or 9·4 for full reproductive life (i.e. sixth to penultimate day inclusive).

In the 12–24 hr. groups old age was usually the apparent cause of death. Two died of rupture of the gut. In one case (20 hr. group, *j*) the oviduct became blocked. This louse, though tensely swollen and unable to lay, lived in this condition for almost a fortnight and is largely responsible for the rather low results obtained in this group. In the 4 and 8 hr. groups the "individual temperament"—the faculty of seizing every opportunity for feeding—became important. Most of the members of these groups died early. Usually one feed was missed and by the time the next was due the louse was too weak to take

the opportunity. This was tested in the case of a few females not included in the experiment. It was found that if these were taken from their boxes in this moribund condition they might often be induced to feed on the wrist by breathing on them gently for a few minutes. If a feed were taken they immediately returned to normal and might live thereafter for a considerable time, but if left to themselves they invariably died. In deaths of this type it is thought that dehydration is at least as important as starvation.

It was noticed that at the final moult quite a large amount of blood might be retained in the gut. The unfed group was started in order to determine whether this blood, along with accumulated food reserve, was sufficient to permit of egg-laying before death. The females of this batch were chosen to include some very large and some very small lice but all died on the third day without laying. Accordingly, this group is omitted from the calculations, except those concerned with longevity.

Longevity

Some difficulty was met in assessing the significance of the figures. The samples are too small for a straightforward application of the standard error test of the difference between means (Hill, 1937, p. 57). The method finally employed was to work out a combined standard deviation for the two groups to be compared and subsequently to determine whether the two means could reasonably be expected to occur within the same universe. As a check, the group totals were also subjected to the test for goodness of fit by χ^2. In every case the results of these two tests were in agreement and the results appear reasonable.

It seems probable that no significant difference in longevity occurs between the 12, 16, 20 and 24 hr. groups, nor between the 4 and 8 hr. groups. Significant differences exist between the unfed and 4 hr. groups and between the 8 and 12 hr. groups. These three main subdivisions are well shown in the histogram (Fig. 1*a*). Thus unfed lice died very early—3 days—and lice fed 4 and 8 hr. daily also had rather short lives, averaging about 13 days. Those fed 12 hr. and over lived, on an average, about 30 days. The longest recorded life was 44 days, a figure which falls far below the maximum of 61 days noted by Buxton (1939).

Rates of laying

The same procedure was adopted in considering the rates of laying and the same conclusions were reached. Again no significant difference was detected between the 12, 16, 20 and 24 hr. groups nor between the 4 and 8 hr. groups. The difference between the 8 and 12 hr. groups was found to be significant (Fig. 1*b*).

It was thought that if only the full reproductive life were considered (from, say, the sixth to the penultimate day inclusive) more evenly graded results might be obtained. This procedure eliminates many lice which died

in the first week, before reaching their full reproductive capacity. The results, however, followed rather closely the same trend as before, the rates being 8·8, 7·6, 7·7, 7·7, 5·9 and 5·2 eggs per louse per day in the 24 to 4 hr. groups respectively. Such being the case, it has seemed preferable to use the entire figures and the whole length of life. The initial lag and the occurrence of early deaths are, after all, part of the general picture.

If in each group every separate day's lay by each louse is noted and if the number of times each figure occurs is summed, the mode (or most frequently occurring number) may be found. If these results are expressed as percentages (Table 3) a more accurate basis for comparison between groups is gained.

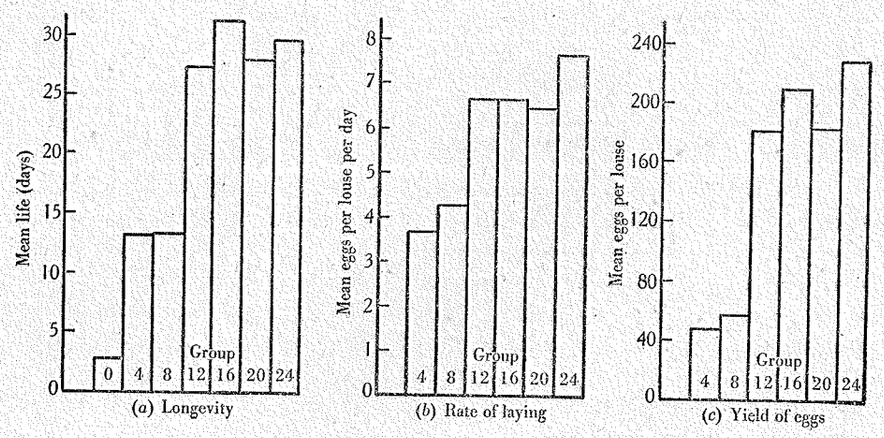

Fig. 1. Mean longevity, rate of laying and yield of eggs. All groups.

Table 3. *Percentage frequency with which different numbers of eggs were laid per day. The mode is in italics: days on which an insect laid no eggs have been omitted in calculating it*

	Number of eggs													
Hours	0	1	2	3	4	5	6	7	8	9	10	11	12	13
24	8·4	1·3	2·4	1·0	2·0	3·0	4·7	7·0	15·4	21·2	*21·5*	8·4	3·0	0·7
20	13·4	2·8	2·1	1·8	5·0	5·7	8·9	9·6	*14·9*	*14·9*	13·8	5·3	1·8	—
16	10·5	1·0	1·9	2·6	3·8	4·1	8·9	12·7	*23·9*	18·1	9·9	2·6	—	—
12	7·6	3·6	0·7	1·5	1·5	7·2	13·8	*19·9*	*19·9*	13·4	8·0	2·9	—	—
8	20·2	2·2	2·2	6·7	13·4	*17·2*	15·8	11·2	6·7	3·7	0·7	—	—	—
4	19·5	8·3	4·5	11·3	11·3	*18·0*	14·3	10·5	0·8	1·5	—	—	—	—

Except for calculation of percentages the days on which an insect laid no eggs are neglected. It is seen that in the series the mode reaches a higher figure progressively with increase in feeding time. The sequence is fairly regular and discloses a serial effect not shown by the means of the groups. Thus, according to the mode the groups present an ascending series instead of two main subdivisions.

Eggs per louse

The figures for eggs per louse show within each group a very wide scatter as they take no account of the length of life. They afford a poor basis for discussion in comparison with the rates of egg-laying. It is thought that, in view of the small size of the samples and the scatter of the results, little reliance can be placed on statistical tests of significance. Such were indeed applied, but without consistent results. A consideration of the histogram (Fig. 1*c*) shows that the results are comparable with those of the preceding section. Thus the 4 and 8 hr. groups may be regarded as similar, as may the 12–24 hr. groups. Possibly the 24 hr. group may be segregated from the 12 to 20 hr. groups, but the evidence is inconclusive.

Conclusion

It is concluded that until the feeding period is reduced to less than 12 hr. per day little decrease occurs in longevity or reproductive activity. Below this level a sharp fall occurs in both. In general, the rates of egg-laying were high, as compared with others that have been recorded (Buxton, 1939, p. 36); the suggested practical application is that where large stocks of lice are being reared the rate of production may be increased by keeping them close to the skin even when they are not feeding. This would appear to be preferable to keeping them in the pocket or in an incubator. Further, in the case of persons who find it injurious or impossible to permit continuous feeding, the feeding period may be reduced to 12 hr. per day without seriously lowering the output of eggs, so long as the boxes are worn constantly under the clothes.

Summary

1. Isolated unmated female body-lice were worn in pillboxes between the skin and the clothes. They were kept constantly on the body but, by a simple device, groups of ten were permitted feeding periods of different length. These groups were fed for 4, 8, 12, 16, 20 and 24 hr. per day respectively. Another group of ten were never allowed to feed after the last moult.

2. Some of the figures for egg yield were high. Lice in the 24 hr. group were able to maintain a rate of ten eggs per day for 4–5 days at a time.

3. No significant difference in longevity or rate of egg-laying was found to exist between the 12, 16, 20 and 24 hr. groups nor between the 4 and 8 hr. groups but a pronounced and significant difference exists between the 8 and 12 hr. groups. Below 12 hr. there is a sharp fall in longevity and rate of egg production. The unfed group all died, without laying, on the third day.

4. The rate of laying as shown by the mode increases progressively with increase in time allowed daily for feeding.

5. With regard to the mean eggs per louse the position is less clear. It is felt that the 24 hr. group may differ significantly from the 12, 16 and 20 hr. groups but this is uncertain.

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