

- Huxley, P. A. (1962). *Physiological and ecological investigations with coffee seeds and seedlings in Uganda*. Ph.D. thesis, University of Reading.
- Huxley, P. A. (1963a). Some growth characteristics of widely spaced plants grown in full daylight in an equatorial climate. *Biochem. J.* 89, 76p.
- Huxley, P. A. (1963b). Solar radiation levels throughout the year for some localities in Africa and elsewhere. *Tech. Bull. Fac. Agric. Makerere Univ. Coll.* 2.
- Huxley, P. A. (1964a). Some factors which can regulate germination and influence viability of coffee seeds. *Proc. int. Seed Test. Ass.* 29, 33-60.
- Huxley, P. A. (1964b). Performance of the Megatron-Siemens integrating photometer in an equatorial climate. *J. agric. Engng Res.* 9, 225-9.
- Huxley, P. A. (1964c). Some effects of artificial shading on the growth of upland cotton seedlings. *Emp. Cott. Grow. Rev.* 41, 100-11.
- Maestri, M. & Gómez, F. R. (1961). Crecimiento de mudas de café (*Coffea arabica* L. var. 'Bourbon') sob diferentes de luz. (The growth of transplanted seedlings of coffee under different light intensities.) *Revta Ceres*, 11, 265-71.
- Machado, A. (1946). Influencia del sombrero et suelo y los practicas de cultivo en el desarrollo del cafeto en sus primeros meses de vida propia; experimento preliminar. (The effect of shade, soil and cultural practices on the early development of the coffee tree.) *Bol. Inf. Cent. nac. Invest. Café Colombia*, 1, 1-32 (*Hort. Abstr.* 21, 3009).
- McClelland, T. B. (1926). Experiments with fertilizers for coffee in Puerto Rico. *Bull. Porto Rico agric. Exp. Stn fed. Stn Mayaguez*, 31.
- McClelland, T. B. (1934). Coffee investigations—shading favours coffee development. *Rep. P. Rico fed. agric. Exp. Stn 1933*, pp. 13-15.
- McClelland, T. B. (1935). Coffee investigations—shading. *Rep. P. Rico fed. agric. Exp. Stn 1934*, pp. 12-14.
- McClelland, T. B. (1937). Coffee investigations—Robusta: shading increases coffee yields. *Rep. P. Rico fed. agric. Exp. Stn 1936*, pp. 71-2.
- Maggs, D. E. (1960). The stability of the growth pattern of young apple trees under four levels of illumination. *Ann. Bot. N.S.* 24, 434-50.
- Monselise, S. P. (1951). Growth of citrus seedlings. I. Growth of Sweet Lime seedlings in dependence upon illumination. *Palest. J. Bot., Rehovot Ser.* 8, 54-75.
- Monteith, J. L. (1959). Solarimeter for field use. *J. scient. Instrum.* 36, 341-6.
- Montoya, L. A., Sylvain, P. G. & Umana, R. (1961). Effect of light intensity and nitrogen fertilization upon growth differentiation balance in *Coffea arabica* L. *Coffee*, 3, 97-104.
- Montoya, L. A. & Umana, R. (1961). Effect of three light intensities and three levels of nitrogen (urea) on incidence of die-back. *Coffee*, 3, 1-5.
- Murray, D. L. (1953). A shade and fertilizer experiment with Cocoa. 11. *Rep. Cacao Res.* 1952, pp. 11-21.
- Njoku, E. (1959). An analysis of plant growth in some West African species. I. Growth in full daylight. *Jl W. Afr. Sci. Ass.* 5, 37-56.
- Njoku, E. (1960). An analysis of plant growth in some West African species. II. The effect of shading. *Jl W. Afr. Sci. Ass.* 6, 1-17.
- Orlando, C. S. (1963). Influencia de siete intensidades de sombra en almácigos de café. (The effects of six shade intensities in coffee nurseries.) *Revta cafet. (Guatem.)*, 23, 6-12 (*Hort. Abstr.* 1965, 4526).
- Rayner, R. W. (1958). *Rep. Coff. Res. Stn Ruiru 1956-7*, pp. 80-8.
- Richards, P. W. (1952). *The Tropical Rain Forest, an ecological study*. Cambridge.
- Robinson, J. B. D. & Bull, R. A. (1961). Debility growth symptoms in Arabica coffee. *Kenya Coff.* 26, 251-5.
- Sturdy, D. (1935). Observations on coffee under artificial shade at Selian Coffee Estate, Arusha, 1931-5. *E. Afr. agric. J.* 1, 135-9.
- Sylvain, P. G. (1952). Effect of shade upon growth and differentiation of coffee seedlings as expressed by physical measurement and chemical composition. Mimeographed report, Inter-American Institute of Agricultural Sciences, Turrialba, Costa Rica.
- Sylvain, P. G. (1958). Coffee shade problems. Inter-American Institute of Agricultural Sciences, Turrialba, Costa Rica; Coffee and Cocoa. Training Material No. 3.
- Tanada, T. (1946). Utilization of nitrates by the coffee plant under different sunlight intensities. *J. agric. Res.* 72, 245-58.
- Trench, A. D. (1932). 'Hot and Cold' disease. *Bull. Dep. Agric. Kenya*, 14.
- Wormer, T. M. & Ebagole, H. E. (1965). Visual scoring of starch in *Coffea arabica* L. II. Starch in bearing and non-bearing branches. *Expl Agric.* 1, 41-53.
- Wormer, T. M. & Firman, I. D. (1961). 'Crinkle-leaf' and 'Hot and Cold' symptoms of coffee in Kenya. *Kenya Coff.* 26, 13-17.

(Received 29 December 1965; revision received 25 November 1966)

## THE DISPERSAL OF CERTAIN SPECIES OF MALLOPHAGA WHICH INFEST THE DOMESTIC FOWL, *GALLUS DOMESTICUS*

BY W. D. RYDER

Department of Agricultural Zoology, University of Newcastle upon Tyne

### INTRODUCTION

The Mallophaga (biting lice) are highly host-specific wingless insects, each species being confined to one host species or to closely related genera, species or subspecies of birds or mammals (Harrison 1928). The entire life cycle is passed on the host. The lice live on or near the skin of the host and are thus protected by the feathers, hair or wool, to which the females attach their eggs. Three nymphal instars precede the adult stage, from which they differ in their smaller size, undeveloped gonads and genitalia, and less extensive chaetotaxy. Most species are parasites of birds, the feathers of which provide a particularly effective layer of insulation near the skin.

This insulation, together with the almost constant body temperature of the host (Wetmore 1922), creates a highly stable microenvironment between the skin and the outer surface of the plumage in which the physical conditions are largely independent of ambient factors.

Table 1. *The numbers of occasions on which Mallophaga were found during visits to seventeen flocks distributed throughout Northumberland, Durham, Cumberland and Westmorland*

Flocks	Numbers of occasions found			
	<i>Menacanthus stramineus</i>	<i>Menopon gallinae</i>	<i>Gonioctes gallinae</i>	<i>Lipeurus caponis</i>
On deep litter (8)	18	9	12	0
In batteries (8)	2	5	0	2
On range (1)	2	2	2	0
Total	22	16	14	2

There is no known stage in the mallophagan life cycle which is specially adapted for dispersal, and the only obvious opportunity for transfer between host individuals occurs when they are directly in contact with one another. This possibility arises in wild birds, for instance during flocking and the rearing of young.

Whilst the conditions may be suitable for the transfer of lice between the domestic fowls in any particular flock, there are no obvious means by which lice may be transferred from one generation of fowls to the next, since it is normal practice to incubate and rear artificially and to keep pullets apart from older birds. It is usual for pullets to be reared partly on range and there is thus a possibility of the transfer of lice from wild Galliformes. When due to begin laying, pullets are most frequently restricted to enclosed accommodation, but occasionally they remain on range so that the possibility of contact with closely related wild genera continues. Although domestic fowls may be introduced to a farm from an outside source, it is usual for such birds to be kept apart from fowls already present, and there is therefore little chance of Mallophaga accompanying their hosts into uninfested flocks.

Table 1 summarizes the results of a survey of the prevalence of Mallophaga in seventeen flocks of laying hens in the north of England, and shows that lice were widely distributed in this region. This fact, and the apparent absence of contact between different generations and flocks of domestic fowls, suggested that the source of the parasites might well be the wild Galliformes inhabiting the localities where the fowls were reared. The subsequent investigation of this possibility is described below.

#### THE PRIMARY SOURCES OF THE MALLOPHAGA WHICH INFEST DOMESTIC FOWLS

Table 2 is a list of the reported alternative hosts of the common mallophagan parasites of the domestic fowl. All the hosts are Galliformes and both *Phasianus colchicus* and *Perdix perdix*, which occurred in the localities covered by the survey, are included. Mallophaga were found on wild examples of these two species as in Table 3; none of

Table 2. The reported alternative hosts of the common mallophagan parasites of the domestic fowl

Louse	Host	Reference
<i>Menacanthus stramineus</i>	Common pheasant ( <i>Phasianus colchicus</i> )	Seguy (1944)
	Domestic turkey ( <i>Meleagris gallopavo</i> )	Emerson (1956)
<i>M. pallidulus</i>	Jungle fowl ( <i>Gallus bankhiva</i> )	Emerson (1956); Emerson & Elbel (1957)
<i>Menopon gallinae</i>	<i>Phasianus</i>	Seguy (1944)
	Domestic guinea fowl ( <i>Numida meleagris</i> )	Emerson (1956)
	Jungle fowl	Emerson & Elbel (1957)
<i>Lipeurus caponis</i>	Common pheasant	Clay (1949)
	Common partridge ( <i>Perdix perdix</i> )	Clay (1949)
	Domestic guinea fowl	Clay (1949)
	Red-legged partridge ( <i>Alectoris rufa</i> )	Seguy (1944)
	Jungle fowl	Emerson (1956); Emerson & Elbel (1957)
<i>Cuclotogaster heterographus</i>	<i>Phasianus</i>	Emerson (1951, 1956)
	<i>Alectoris</i>	Emerson (1956)
<i>Lipeurus tropicalis</i>	Jungle fowl	Emerson (1956)
<i>Gonioctes gallinae</i>	Domestic guinea fowl	Seguy (1944)
	Jungle fowl	Emerson (1956); Emerson & Elbel (1957)
<i>Goniodes gigas</i>	Domestic guinea fowl	Emerson (1956)
<i>G. dissimilis</i>	Domestic guinea fowl	Emerson (1956)
	Jungle fowl	Emerson (1956); Emerson & Elbel (1957)
<i>Oxylpeurus dentatus</i>	Jungle fowl	Emerson (1956); Emerson & Elbel (1957)

Table 3. Mallophaga recovered from *Phasianus colchicus* and *Perdix perdix*

Hosts	Mallophaga
<i>Phasianus colchicus</i> (60 birds)	<i>Gonioctes chrysocephalus</i>
	<i>Goniodes colchici</i>
	<i>Cuclotogaster heterographus</i>
	<i>Lipeurus</i> sp., probably <i>maculosus</i>
	<i>Amyrsidea</i> sp.
<i>Perdix perdix</i> (12 birds)	Nil

these lice were found on domestic fowls in the area, and only *Cuclotogaster heterographus* is common to Table 2 and Table 3. It thus seems unlikely that wild Galliformes were a source of the regular mallophagan parasites of these domestic fowls. The domestic turkey *Meleagris gallopavo* was also a possible alternative host, and the only flock examined was in fact infested with *Menacanthus stramineus*. There was, however, no evidence of contact between domestic fowls and turkeys in the area.

It thus seemed probable that the only primary sources of the Mallophaga in question were the domestic fowls themselves and perhaps domestic turkeys. The acquisition of Mallophaga by flocks of domestic fowls remained unexplained, and an attempt was therefore made to discover if viable lice occurred in extra-host situations near to domestic fowls.

#### SAMPLING IN EXTRA-HOST SITUATIONS FOR MALLOPHAGA

In the same seventeen flocks an examination was made, at 3-monthly intervals for 1 year, of the cages in battery units, and of the perches, the nest-box interiors, the remaining woodwork and the litter in deep-litter and range houses. The only mallophagan parasite recovered was a headless specimen of *Menopon gallinae*, and there was thus no evident tendency for the lice to stray from the host. The possibility that the lice were transmitted between the primary hosts by vector agencies was therefore considered.

#### VECTOR TRANSMISSION OF MALLOPHAGA

In the hen houses, examples of *Passer domesticus* and *Hirundo rustica* were trapped and sampled for ectoparasites using Williamson's (1954) technique, and nest linings of these species were examined. Continual watch was maintained for possible louse-carrying Hippoboscidae (Ansari 1946) on c. 400 domestic fowls examined between June and September, the reported period of activity of the group (Thompson 1937), and two sticky fly traps (Ibbotson 1958) were sited in a house containing hens infested with *Menacanthus stramineus*. None of these measures resulted in the discovery of either regular mallophagan parasites of the domestic fowl or of Hippoboscidae. Hoyle (1938), however, found *Cuclotogaster heterographus* as a straggler on *Passer domesticus*, and showed experimentally that *Menopon gallinae* could survive for at least 9 days and breed on this host. Nevertheless, in the present study there seemed little chance that Mallophaga could be transmitted from flock to flock as stragglers on wild birds, or on other insects.

It was found that when domestic fowls infested with *Menacanthus* were handled, some of the lice crawled on to the handler's clothing and skin, where they remained alive for at least 5 h. This suggested that human agency was the main factor responsible for the transmission of lice between flocks managed by the same poultryman, whilst the wider dissemination of the parasites was probably accounted for by inter-farm movements of stock.

To allow for the eventuality that a small undetected population of lice did occur in extra-host situations, it was decided to investigate certain aspects of the biology of the lice in controlled environments. A necessary preliminary to this work was the consideration of the physical environment both on and surrounding the host, and appropriate observations were made at the previous sites.

## THE PHYSICAL ENVIRONMENT OF THE MALLOPHAGA

## On the domestic fowl

Wetmore (1922) showed that the internal body temperature of the domestic fowl varied in a diurnal rhythm from a daytime maximum of 41.9° C to a night-time minimum of 40.8° C, regardless of the atmospheric temperature. In the present work, temperatures varying between 35 and 38° C and between 30 and 35° C were recorded on and at 0.5 cm above the skin respectively. No measure of relative humidity or light intensity beneath the surface of the plumage was obtained, but it seems likely that these factors also would be stable.

Table 4. Frequency distribution of mean temperatures recorded inside houses and in the open air

Temperature range (°C)	Numbers of occasions recorded	
	Inside houses	Open air
0-2	0	2
3-4	1	2
5-6	1	7
7-8	7	8
9-10	11	7
11-12	6	8
13-14	11	9
15-16	8	2
17-18	2	5
19-20	4	4
21-22	2	0
23-24	2	0
25-26	0	1

Table 5. Frequency distribution of mean relative humidities recorded inside houses and in the open air

Relative humidity range (% R.H.)	Numbers of occasions recorded	
	Inside houses	Open air
46-50	1	3
51-55	1	2
56-60	2	2
61-65	2	2
66-70	4	1
71-75	9	12
76-80	13	4
81-85	10	9
86-90	10	11
91-95	2	5
96-100	1	4

## In extra-host situations

## (i) Atmospheric temperature and relative humidity

Tables 4 and 5 summarize the temperature and relative humidity data derived from psychrometer readings taken on different occasions throughout one year at the seventeen sites. Approximately 90% of the temperatures recorded in the open air lay in

the range 5-20° C, whilst a similar percentage of the temperatures recorded in hen houses lay in the range 7-20° C. Approximately 80% of the relative humidity records in both situations lay in the range 71-95% R.H.

## (ii) Litter temperature

Table 6 summarizes the data relating to the temperature at the bottom of the litter in deep-litter houses and shows that approximately 70% of the records lay in the range 13-18° C.

Table 6. Frequency distribution of temperature at full depth of litter

Temperature (°C)	No. of occasions recorded
7	1
8	1
9	2
10	1
11	3
12	3
13	8
14	2
15	5
16	4
17	11
18	10
19	4
20	2
21	2
22	1
23	0
24	1
25	1

Table 7. Frequency distribution of percentage moisture content of litter

Range of moisture content (%)	No. of occasions recorded
0-5	6
6-10	8
11-15	19
16-20	16
21-25	29
26-30	18
31-35	11
36-40	10
41-45	10
46-50	11
51-55	5
56-60	2
61-65	0
66-70	0
71-75	1

## (iii) Moisture content of litter

Samples of litter were extracted using Murphy's (1958) modified Berlese apparatus, and the loss in weight was ascribed to water evaporated during the process. Table 7 summarizes the derived data and shows that approximately 85% of the records lay in the range 11-50% moisture content.

## (iv) Light intensity

Table 8 summarizes the records of light intensity and shows that most of the values obtained in the open air were above 100 ft-candles, whilst most of those obtained in hen houses were below 30 ft-candles, with numerous much lower values, particularly in battery accommodation.

Table 8. Frequency distribution of mean light intensities recorded inside houses and in the open air

Site	No. of records within the following ranges of light intensity (ft-candles):			
	0-10	10-30	30-100	> 100
Deep-litter houses (8) and range house (1)	17	7	2	0
Batteries (8)	95	12	1	0
Open air	0	0	15	30

## Differences between host and extra-host environments

From the above observations it is clear that Mallophaga which quit the domestic fowl host will experience substantial decreases in temperature and increases in light intensity, the former unaffected by the site of displacement but the latter relatively accentuated in the open air. To assess the importance of these changes, the survival and behaviour of *Menacanthus* in relevant sets of physical conditions were subsequently investigated.

THE BIOLOGY OF *MENACANTHUS STRAMINEUS* EX HOST

## Survival

## (i) Effects of temperature and humidity on length of survival

Immediately after removal from the host, adult lice were held individually for multiples of 8 h at temperatures of 7, 9, 13, 21 and 31° C and at relative humidities of 1, 25, 50, 75 and 100% R.H. in all possible combinations. Each louse was contained in an unsealed

Table 9. The maximum period of survival for twenty-five adults of *Menacanthus stramineus* at different temperatures

Temperature (°C)	Survival period (h)
7	36 ± 4
9	44 ± 4
13	44 ± 4
21	52 ± 4
31	28 ± 4

glass tube and there were five replicates of each treatment. After the treatments the tubes were placed at 35° C beneath a bench lamp and the lice were examined frequently for 2 h. Death was assumed if no movement was observed. The lice were finally sexed on the basis of a distinctive sexual dimorphism in the abdominal chaetotaxy which was illustrated by Emerson (1956).

There was no evident humidity effect, and the results are summarized with respect to temperature in Table 9, which shows that the longest survival period, 52 ± 4 h, occurred

at 21° C. This contrasts with the temperature preferendum of 28-36° C as determined below, and with the optimum survival temperature of 35° C as determined by Stockdale & Raun (1965). It seems possible that at 31° C an additional factor entered the experiment and caused the relatively short survival period of 28 ± 4 h. Alternatively, the temperature of 21° C may have been that at which the lice could survive longest without food. The work of Wilson (1934, 1939) on *Cuclotogaster heterographus* and *Lipeurus caponis*, and that of Stockdale & Raun, suggests that the length of survival of Mallophaga in the absence of the host is partly determined by the availability of food.

Ten adult lice were exposed in an unsealed glass tube at 19° C to each of the relative humidities used previously, and the mortality was recorded at frequent intervals. The numbers of additional lice dead at each inspection were summed for the three replicates obtained at each humidity. The summarized results in Table 10 confirm that there was no appreciable humidity effect on survival.

Table 10. Additional mortality at each successive inspection of *Menacanthus stramineus* adults held at different humidities

Time of inspection (h)	Additional lice dead at the following relative humidities (%):				
	1	25	50	75	100
4	2	1	0	2	2
16	5	1	5	2	6
20	3	8	7	2	4
24	5	6	8	6	2
30	3	4	7	7	2
40	9	10	2	10	12
42	3	0	1	1	2

Table 11. The temperature of revival of *Menacanthus stramineus* adults after exposure to 5° C for varying periods (temperature raised at 1° C per minute)

Specimen	Temperature (°C) of revival after exposure for (h):										
	½	¾	1	1½	2	2½	3½	5	20	25	
1	8.2	8.5	15.0	19.5	24.0	29.9	32.5	37.1	42.9	44.5	-
2	9.0	9.3	15.0	20.0	24.0	30.0	32.9	38.2	45.9	-	-
3	9.0	9.7	16.0	20.5	24.2	30.0	36.2	38.3	47.0	-	-
4	9.9	9.8	17.0	20.8	28.7	30.6	37.1	38.6	47.2	-	-
5	11.2	10.8	17.0	20.8	29.3	32.2	37.3	38.9	-	-	-
Means	9.5	9.6	16.0	20.3	26.0	30.5	35.2	38.2			

## (ii) Revival after exposure to low temperature

It was observed that cold stupor ensued in adult lice on lowering the environmental temperature to 7° C. Five lice were then maintained individually in unsealed glass tubes at 5° C for periods of 5, 10 and 20 min and 1, 1½, 2, 2½, 3½, 5, 20 and 25 h, after which the temperature was raised at 1° C per minute and that at which leg movement began in each louse was recorded. The humidity was uncontrolled.

Fig. 1 shows that the longer a louse was maintained at 5° C, either the slower was its response to an increase in temperature or the higher was the temperature necessary to induce revival. Maximum revival occurred after exposures of 3½ h or less, whilst after the 25-h exposure there was no revival. The results are detailed in Table 11.

Batches of ten adult lice were maintained in individual unsealed glass tubes at 6° C

and 75% R.H. for periods of 1/2, 1, 2 and 4 h at the end of which the temperature was raised in 30 sec to 20° C. A record was kept of the time at which leg movement was resumed in each louse, and Fig. 2 shows that the lice responded to the temperature increase after a

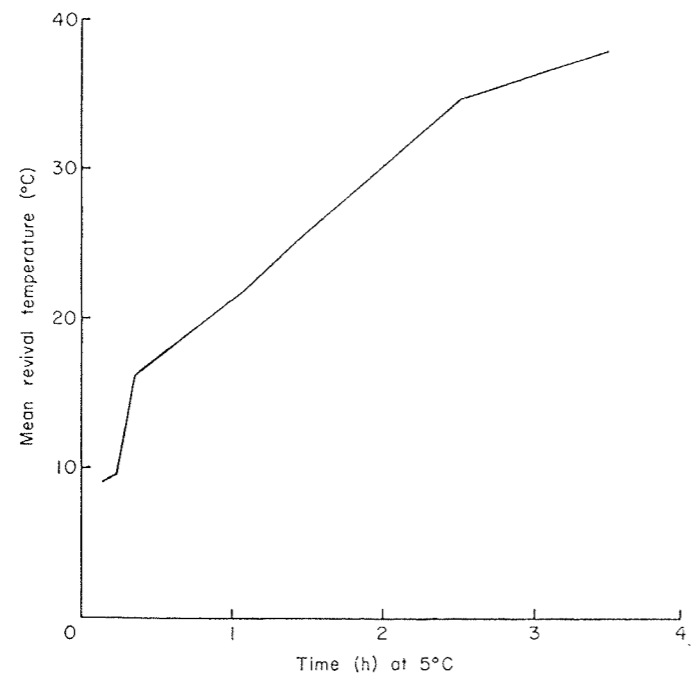


FIG. 1. Mean revival temperature of batches of five adult *Menacanthus stramineus* after varying periods of exposure to a temperature of 5° C.

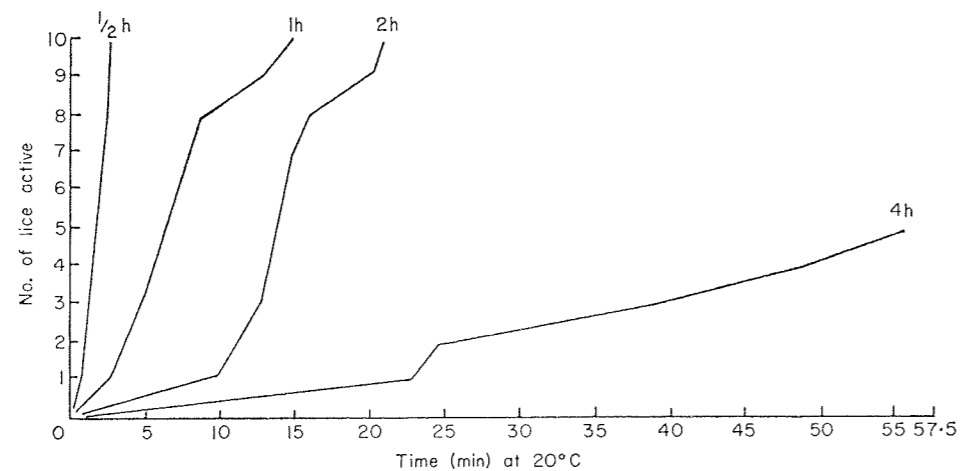


FIG. 2. Rate of revival in batches of ten adult *Menacanthus stramineus* on raising the temperature to 20° C after exposure to a temperature of 6° C for varying periods.

delay which increased with the period of exposure. Of the specimens exposed for 4 h, only half revived, and they did so only partially and temporarily, so that it appeared unlikely that cold stupor could be a survival mechanism.

(iii) *Survival of eggs*

It was observed that there was a small percentage hatch from egg clusters removed from domestic fowls and held for 11 days at 36° C and 85% R.H. This suggested that egg clusters might provide an effective means of dispersal in the field, but no confirmatory evidence was obtained.

*Behaviour*

(i) *Temperature reactions*

Batches of ten adult lice of each sex were transferred from the host to environments in which a dorsal light intensity of 18 ft-candles was combined with temperatures of 15.5, 18 and 28° C. The paths of the lice were traced in pencil for 1 min and linear and angular measurements were made (Ullyott 1936). Table 12 shows that for each batch, linear

Table 12

(a) *The distances travelled by ten adult Menacanthus stramineus of each sex in 1 min at various temperatures*

Temperature	Distance travelled (cm)										Mean
	1	2	3	4	5	6	7	8	9	10	
15.5° C											
Male	15.0	15.5	15.5	16.0	16.0	16.0	16.5	16.5	16.5	17.0	16.1
Female	13.5	14.0	14.5	15.0	15.0	16.0	16.0	16.5	16.5	17.5	15.5
18.0° C											
Male	24.0	25.0	25.5	26.0	26.0	27.0	27.5	28.0	28.0	29.0	26.6
Female	18.0	19.5	20.0	20.5	21.0	21.5	23.0	23.5	24.0	25.5	21.7
28.0° C											
Male	63.0	66.0	69.5	75.0	77.0	78.5	79.0	79.5	81.0	84.5	75.3
Female	54.5	56.0	58.0	61.0	61.5	65.0	66.0	71.0	71.5	73.0	63.8

(b) *The angles turned by ten adult Menacanthus stramineus of each sex in 1 min at various temperatures*

Temperature	Angle turned (degrees)										Mean
	1	2	3	4	5	6	7	8	9	10	
15.5° C											
Male	879	964	1013	1059	1234	1296	1300	1370	1431	1634	1218
Female	831	913	973	981	1172	1189	1249	1286	1379	1598	1172
18.0° C											
Male	214	287	374	395	448	596	638	652	731	876	521
Female	226	249	354	367	412	423	580	632	640	795	467
28.0° C											
Male	164	187	223	265	288	317	374	386	419	420	304
Female	139	151	198	232	248	272	331	358	359	397	269

movement increased and the angle of turn decreased with increase in temperature. Such behaviour in lice displaced from the host in field conditions would clearly tend to prevent appreciable dispersal.

A sealed, thin-walled glass tube measuring 30 × 1 cm and containing ten adult lice was immersed horizontally in water giving a temperature gradient from 14 to 39° C. The position of the lice relative to the temperature was observed after 10 min in three replicates of the experiment, and it was found that the lice always aggregated in the range 28–36° C.

This preferendum approximates to the temperature range in the natural environment, where the reactions described above would tend to maintain the lice. Wigglesworth (1941) demonstrated similar behaviour in the human body louse *Pediculus humanus*, and showed that when half of an arena was above the preferred temperature of 30° C and the other half was below, a louse could orientate along the boundary by swinging the head and the antennae to right and left alternately as it moved forward.

(ii) *Light reactions*

With a uniform temperature of 15° C the paths were traced, for 1 min, of ten adult lice in each of five batches subjected respectively to dorsal light intensities of 0.2, 2.4, 9.8, 46.0 and 100+ ft-candles. Linear and angular measurements were made, and the derived means are given in Table 13. Linear movement and angle of turn were both

Table 13. *The mean distance travelled, mean angle turned and mean number of degrees turned per centimetre of linear movement for ten adult Menacanthus stramineus at various light intensities for 1 min*

Light intensity (ft-candles)	Mean distance travelled (cm)	Mean angle turned (degrees)	Mean angle turned per cm linear movement (degrees)
0.2	10.3	1949	194
2.4	9.8	2503	253
9.8	13.1	2651	202
46.0	14.2	2535	178
100+	16.8	2112	125

Table 14. *The mean distance travelled and the mean angle turned per centimetre of linear movement in each of six successive groups of five 1-min observations on adult Menacanthus stramineus at a light intensity of 18 ft-candles and a temperature of 15° C*

	Group					
	1	2	3	4	5	6
A. Male louse						
Mean distance travelled (cm)	17.1	12.6	9.9	7.4	6.1	5.9
Mean angle turned per cm linear movement (degrees)	66	86	89	120	101	110
B. Female louse						
Mean distance travelled (cm)	14.0	14.2	10.1	6.2	5.3	4.7
Mean angle turned per cm linear movement (degrees)	52	49	63	89	94	68

relatively low only when the dorsal light intensity was 0.2 ft-candles, which illumination was probably the closest to that in the natural environment. The mean angle of turn per centimetre of linear movement was relatively high at 0.2 ft-candles, and was greatest at 2.4 ft-candles, the net effect being that at the higher light intensities the lice tended to move further without turning.

At a temperature of 15° C and a dorsal light intensity of 18 ft-candles, the paths of two adult lice were traced for alternate 1-min periods in 1 h. Table 14 shows that the rate of linear movement tended to decrease whilst the angle of turn per centimetre of linear movement tended to increase with time. Thus the lice were progressively less likely to move far from their point of deposition.

Using dark-room facilities at a temperature of 15° C, the paths were traced of adult lice placed 1 cm from the middle of the base of a 1-in. square window admitting daylight to a horizontal plane. Fig. 3 is a typical tracing: the lice crawled away from the window on

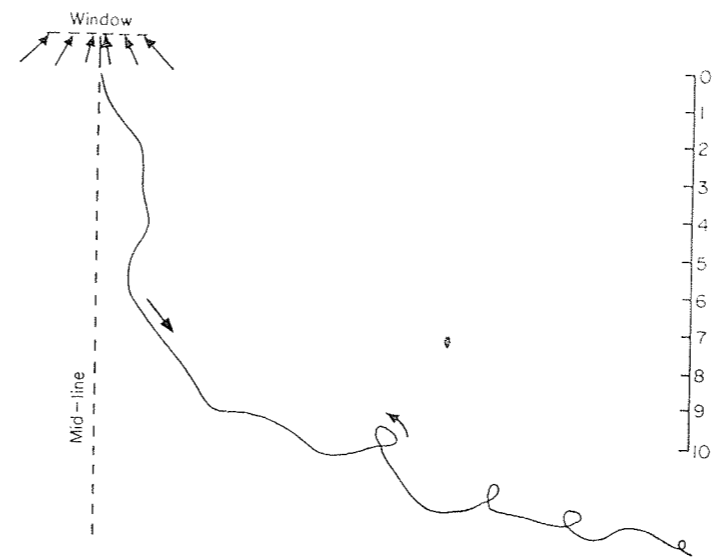


FIG. 3. Path taken by an adult *Menacanthus stramineus* in diverging light rays emanating from a small daylight source in a dark room.

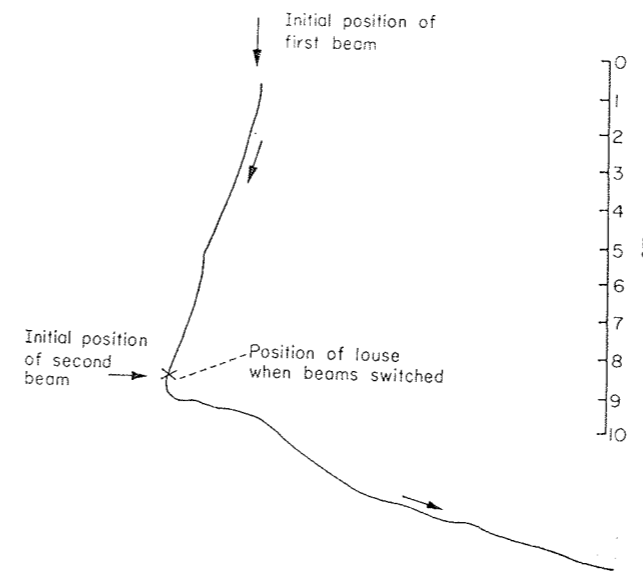


FIG. 4. Path taken by an adult *Menacanthus stramineus* in two successive light beams at right angles to one another.

either side of the mid-line and at a variable angle to it which increased progressively; frequent movements were made in a loop towards the window, each continuing until the original course was resumed. The paths closely resembled those taken by organisms

which maintain a fixed angle of orientation to the divergent light rays from a source in their immediate vicinity (Fraenkel & Gunn 1961).

Two light beams which intersected at right angles were projected by means of two 100-W slit sources on to a horizontal wooden board. Single adult lice were exposed to the two beams in succession, and were maintained continuously in one or the other of them. Several tracings were obtained for each specimen, and a typical result is illustrated in Fig. 4. The lice travelled away from the initial source at a fixed left or right angle to the beam, whilst on substitution of the second source re-orientation occurred so that the new path bore a similar relation to the new beam, as is shown in Table 15. The paths of individual lice were similar in successive tracings. Thus again each louse tended to maintain a fixed angle of orientation to the light rays.

Table 15. *The mean angles of the paths of adult Menacanthus stramineus to an initial light beam and to a second beam at right angles to the first, for six successive trials per louse*

Specimen	Mean angle to initial beam (degrees)	Mean angle to second beam (degrees)
A. Male	41	41
B. Male	22	6
C. Male	10	11
D. Male	26	22
E. Female	22	16
F. Female	24	23
G. Female	54	57

#### *Biology ex host and dispersal*

In the above investigations, the physical changes to which the lice were subjected were largely comparable with those which would occur in the field, where, it may be deduced, abandonment of the host is unlikely, due to the observed responses to temperature and light. The observations suggest that if the lice do reach extra-host situations they will tend to enter dark cryptic niches, where further contact with the host would be improbable, and will die in a short time. The eggs of *Menacanthus* may provide a means of dispersal, but nymphs emerging in extra-host situations would probably be subject to similar adversities. Thus it is confirmed that only contact between birds, or the interposition of a human agent, are likely to facilitate the local spread of the lice.

#### ESTABLISHMENT OF INFESTATIONS OF *MENACANTHUS STRAMINEUS*

##### *Minimum initial population*

Hens were accommodated individually in 1 × 2 × 2 ft wooden boxes lined with wheat straw. The interior of the hen house was inaccessible to wild birds; sticky traps were used to control flying insects; and a strict level of general hygiene was maintained. Adult lice were transferred from heavily infested birds to uninfested ones in the following treatments, all applications being made to the skin near the vent:

- (a) one female per bird (three replicates);

- (b) one male and one female per bird (six replicates);  
(c) two females per bird (six replicates).

All birds were examined after 1, 2 and 3 weeks, and those in treatment (b) were examined after a further period of 3 weeks. The results are given in Table 16, which suggests that if a single gravid female louse reaches a host the establishment of an infestation is likely to follow.

Table 16. *Observations on populations of Menacanthus stramineus on artificially infested domestic fowls*

Treatment	Observed populations after (weeks):			
	1	2	3	6
(a) 1 ♀ louse per bird (3 replicates)	0	0	0	Not observed
(b) 1 ♂ and 1 ♀ louse per bird (6 replicates)	0	Replicate (i): 11 Replicate (ii): 4 Others: 0	Increase observed	Replicate (i): 50+ Replicate (ii): 50+ Others: 0
(c) 2 ♀ lice per bird (6 replicates)	0	0	Replicate (i): 10 Replicate (ii): 15 Others: 0	Not observed

Table 17. *Observations on populations of Menacanthus stramineus on initially uninfested domestic fowls subjected to varying degrees of exposure to infestation*

Treatment	Observed populations after (days):			
	1	7	14	21
(a) Initially uninfested and infested birds in adjacent boxes (6 replicates)	Not examined	0	0	0
(b) Replacement of infested by uninfested birds immediately, and after 24 and 48 h (6 replicates each)	Not examined	0	0	0
(c) Initially uninfested and infested birds placed in the same box (2 replicates)	(i): 6 (ii): 11	Not examined subsequently		
(d) (i) Egg clusters on ceiling of initially uninfested bird's box (6 replicates)	Not examined	0	0	0
(ii) Egg clusters on sides of initially uninfested bird's box (9 replicates)	Not examined	0	0	0
(iii) Egg clusters on tibiae of initially uninfested bird (3 replicates)	Not examined	0	(i): 1 Others: 0	0

##### *Proximity of infested to uninfested birds*

(a) Twelve boxes containing single heavily infested and uninfested birds alternately were arranged in contact with one another. After 2 weeks they were separated and the initially uninfested birds were examined immediately and after 1, 2 and 3 further weeks had elapsed.

(b) Heavily infested birds were removed from their boxes and replaced with uninfested birds immediately and after 24 and 48 h (six replicates per treatment). Examination of the latter birds was carried out after 1, 2 and 3 weeks.

(c) A heavily infested bird and one uninfested were placed together in the same box

(two replicates). An examination of the initially uninfested bird was made after 24 h.

(d) Two small feathers bearing egg clusters were detached from a heavily infested bird and fixed (i) to the upper inside surface and (ii) to the lateral inside surface of an uninfested bird's box (six and nine replicates respectively); (iii) to each tibia of an uninfested bird (three replicates). The birds were examined after 1, 2 and 3 weeks.

The results of these treatments are given in Table 17, which indicates the relative efficacy of direct contact between host individuals in facilitating local dispersal of the lice, the completely negative influence of lesser degrees of proximity of infested to uninfested birds, and the inefficacy of feathers bearing egg clusters as instruments of dispersal.

#### SUMMARY

Sampling for Mallophaga indicated that those species occurring on the domestic fowl in northern England, of which *Menacanthus stramineus* was the commonest, did not normally leave the host, and this was confirmed by *in vitro* experiments. Away from the host *Menacanthus* exhibited a low viability and an apparent tendency to enter dark cryptic situations, with the result that there was little chance of displaced lice initiating infestations. Observation suggested that human agency was an important factor in the local spread of the lice, whilst inter-farm movements of fowls were likely to facilitate wider dispersal. The facility with which infestations were established from very small initial numbers, and the spread of the lice within the flock as a result of contact between birds, would ensure rapid subsequent increases in louse populations.

#### ACKNOWLEDGMENTS

The author is grateful to Dr T. Clay for the identification of the Mallophaga, and to Dr A. Ibbotson for advice and criticism.

#### REFERENCES

- Ansari, M. A. R. (1946). Association between the Mallophaga and the Hippoboscidae infesting birds. *J. Bombay nat. Hist. Soc.* 46, 509-16.
- Clay, T. (1949). Some problems in the evolution of a group of ectoparasites. *Evolution, Lancaster, Pa.* 3, 279.
- Emerson, K. C. (1951). A list of Mallophaga from gallinaceous birds of North America. *J. Wildl. Mgmt.* 15, 193-9.
- Emerson, K. C. (1956). Mallophaga occurring on the domestic chicken. *J. Kans. ent. Soc.* 29, 63-79.
- Emerson, K. C. & Elbel, R. E. (1957). New records of Mallophaga from wild chickens. *J. Parasit.* 43, 381-2.
- Fraenkel, G. & Gunn, D. L. (1961). *The Orientation of Animals: Kineses, Taxes and Compass Reactions*, revised edn. New York.
- Harrison, L. (1928). Host and parasite. *Proc. Linn. Soc. N.S.W.* 53, ix-xxxi.
- Hoyle, W. L. (1938). Transmission of poultry parasites by birds with special reference to the 'English' or house sparrow and chickens. *Trans. Kans. Acad. Sci.* 41, 379-84.
- Ibbotson, A. (1958). The behaviour of frit fly in Northumberland. *Ann. appl. Biol.* 46, 474-9.
- Murphy, P. W. (1958). The quantitative study of soil meiofauna (1). *Entomologia exp. appl.* 1, 94-108.
- Seguy, E. (1944). *Faune de France: Insectes ectoparasites de France*. Paris.
- Stockdale, H. J. & Raun, E. S. (1965). Biology of the chicken body louse, *Menacanthus stramineus*. *Ann. ent. Soc. Am.* 58, 802-5.
- Thompson, G. B. (1937). The parasites of British birds and mammals (2). Records of *Ornithomyia* species from British birds. *Entomologist's mon. Mag.* 73, 47.
- Ulliyott, P. (1936). The behaviour of *Dendrocoelum lacteum*. *J. exp. Biol.* 13, 253-78.
- Wetmore, A. (1922). A study of the body temperature of birds. *Smithson. misc. Collns.* 72, 1.

- Wigglesworth, V. B. (1941). The sensory physiology of the human louse *Pediculus humanus corporis*. *Parasitology*, 33, 67-109.
- Williamson, K. (1954). The Fair Isle apparatus for collecting bird ectoparasites. *Br. Birds*, 47, 234-5.
- Wilson, F. H. (1934). The life cycle and bionomics of *Lipeurus heterographus* Nitzsch. *J. Parasit.* 20, 304-11.
- Wilson, F. H. (1939). The life cycle and bionomics of *Lipeurus caponis* (Linn.). *Ann. ent. Soc. Am.* 32, 318-20.

(Received 14 March 1966; revision received 24 November 1966)