THE ECOLOGY OF LICE ON SHEEP

V. INFLUENCE OF HEAVY RAIN ON POPULATIONS OF DAMALINIA OVIS (L.)

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Summary

Exposure of nymphal and adult *Damalinia ovis* (L.) to 100% R.H. at 37°C did not increase the death rate but immersion for 6 hr in water followed by exposure to 40% R.H. was sufficient to kill all nymphs and adults. Immersion of only 1 hr was fatal for 50–100% when followed by exposure of 7½–24 hr to 90% R.H. Eggs continued to develop under water at 37°C and an appreciable mortality occurred only after 7 days immersion. Exposure to relative humidities of over 90% killed hatching eggs.

When the fleece of a sheep infested with *D. ovis* is soaked by rain it may take many hours to dry and there is a resultant mortality of nymphal and adult lice and hatching eggs. In the region where the experiments were carried out, sheep were soaked periodically by thunderstorms in the autumn. The irregular mortalities of lice on different sheep was reflected 6 months later, when the lousiest sheep were shown to be those which were not soaked in the previous autumn.

I. INTRODUCTION

During the present study of the ecology of lice on sheep it has been observed repeatedly in the field that after the fleece has been soaked with water during heavy rainstorms there is a decline in the number of *Damalinia ovis* (L.). The influence of free moisture on the stages of the life cycle of *D. ovis* has been studied, and the results which are reported in this paper afford an explanation of the effect of rain. They also provide evidence that the number of *D. ovis* found on sheep at the end of winter and in early spring can be dependent on the size of the population at the end of the previous autumn.

II. OBSERVATIONAL

(*a*) *Methods*

Sheep were examined at 20–30 sites on each side of the body to assess the abundance of lice. According to the number of lice seen when 3–4 in. of the fleece of a sheep was parted, the degree of infestation was graded as shown in Table 1. When it was not possible to grade an infestation exactly it was recorded as being either about (*c.*) or slightly greater than (+) the appropriate grade. After the infestation had been graded, the fleece was shaved from an area of 9 sq in of skin and all the living lice in the wool sample counted. This sampling was repeated twice and the relationship between the grades of infestation and the number of lice present was

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established (Table 1). The surface area of the skin of the sheep which is covered with wool was estimated by considering the body to be a cylinder to which a cone, the head and neck, was attached. The required lengths and circumferences were measured on the sheep with a tape measure. The average surface area of the type of sheep used was 1800–2250 sq in. Thus, multiplication of the average number of lice in 9 sq in by 200–250 gave an estimate of the number of lice on the sheep (Table 1).

TABLE 1
ESTIMATION OF NUMBER OF D. OVIS ON SHEEP

Grade of Infestation	No. of Lice Seen on Each Occasion the Fleece Was Parted	Mean No. of Lice on 9 sq in of Skin	Estimated No. of Lice on Sheep*
0	0	0	0
1	Only 1 louse seen on whole sheep	n.d.†	n.d.†
2	1	18	3,600 – 4,500
3	1 (with several pockets of 5 lice)	120	24,000 – 30,000
4	5	220	44,000 – 55,000
5	5 (with several pockets of 10 lice)	630	126,000 – 158,000
6	10	1800	360,000 – 450,000
7	>10 (many nymphs visible)	n.d.†	500,000 – 1 million

* i.e. number per 9 sq in multiplied by 200–250.
† n.d., not determined.

(*b*) *Results*

Four infested Merino sheep with grade 3 infestations and carrying fleeces 2–3 in. long were selected. Three possessed an open type of non-greasy fleece and the fourth a compact greasy fleece. They were placed in a paddock which had no shelter from the weather for 4 weeks during which several rainstorms thoroughly soaked the non-greasy fleeces making them scoured in appearance, with extensive wool discoloration due to fleece rot. The number of lice on these sheep declined to grade 1 infestations, and many dead lice were seen in the fleece. On the other hand, the fleece of the greasy-woolled sheep was not soaked and no such mortality occurred.

A group of 14 infested sheep with infestations of grades 4–6 were shorn in the spring and by the late summer the infestations had declined to *c.* grade 2. During 1 month of the autumn there were many heavy rainstorms, and at the end of autumn, 1–2 weeks after the last rainstorm, the fleeces of all sheep showed evidence of having been soaked and many dead lice were found near the skin. The infestations on six sheep were grade 0, on four grade 1, and on the remaining four grade 1+. All of

these animals were examined 6 months later in the following spring when the infestations of 3 of the 4 sheep which were previously grade 1+ were still grade 1+, and no lice were found on the fourth sheep. Of the remaining 10 sheep, three had grade 1 infestations and seven grade 0.

Seven other sheep, which had not been exposed to the rainstorms, were also examined at the end of autumn, and all of their infestations were graded *c.* 2 – *c.* 3. They were added to the flock, and 6 months later the infestations of six of these sheep were graded 4–6.

III. Experimental

(*a*) *Methods*

The techniques used to collect and handle the various stages of *D. ovis*, to determine the age and time of hatching of eggs, and to control and measure temperature and humidity were described previously (Murray 1957, 1960).

Table 2
Percentage mortality of nymphal and adult D. ovis after exposure to 54, 90, and 100% R.H. at 37°C for 24 hr

Relative Humidity (%)	Sex of Louse	Total No. of Lice	Mortality (%)
54	Male	121	45·4
	Female	335	8·1
	Nymphs	378	17·7
90	Male	296	51·7
	Female	291	6·2
	Nymphs	278	9·7
100	Male	287	55·7
	Female	285	10·2
	Nymphs	410	10·0

(*b*) *Effect of High Humidity*

(i) *Survival of Nymphs and Adults.*—Separate collections of nymphs and adult males and females were each divided into three groups which were placed on filter paper in small petri dishes and exposed to 37°C. One group of each collection was exposed to 54% R.H., another to 90% R.H., and the third to 100% R.H. After 24 hr the living and dead lice were counted. The experiment was repeated twice and similar mortalities occured at each humidity. Males died sooner than nymphs or females (Table 2). The collections of nymphs contained all three instars and there was no differential mortality.

(ii) *Hatching of Eggs.*—It has been shown previously that exposure of the eggs of *D. ovis* to R.H.'s of over 90% during the last 24 hr of development prevents

hatching (Murray 1960). Further experiments were carried out to determine more precisely when this lethal effect operated and the minimal exposure to a high R.H. which could be lethal.

Female lice were collected, placed on wool, and exposed to 37°C at 54% R.H. The eggs which they laid were collected 24 hr later and were returned to 37°C at 54% R.H. On the ninth day they were examined, and the eggs which were expected to hatch within 24 hr were divided into two groups, and returned to 37°C at 54% R.H. They were then examined at hourly intervals, and when hatching commenced, the eggs of one group were exposed for alternate 3-hr periods to dry air over calcium chloride or to *c.* 100% R.H. By this method, the R.H. of the air surrounding the eggs rose above or fell below 90% within 1 min. The eggs, which were individually

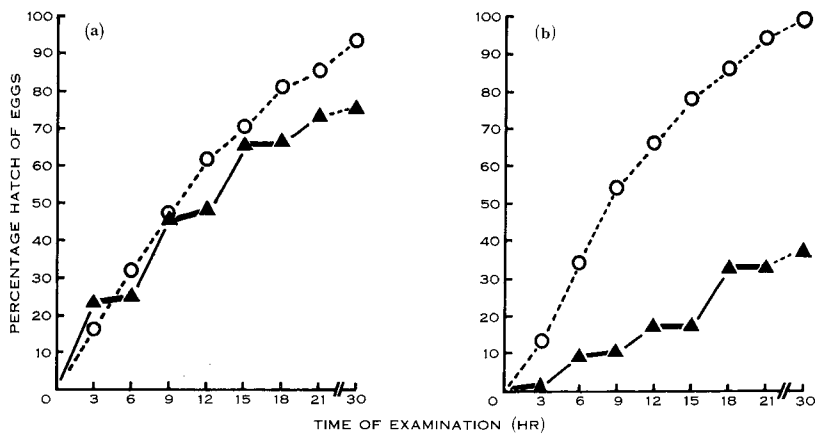

Fig. 1.—Influence of exposure to high humidity on the hatching of the eggs of *D. ovis*: - - - exposed to 37°C at 54% R.H.; — exposed to 37°C in dry air (over calcium chloride); ▬ exposed to 37°C in moist air (*c.* 100% R.H.).

identified, were examined through the clear glass lids of the containers at intervals of 3 hr to determine the number which had hatched. The experiment was repeated and Figures 1(*a*) and 1(*b*) show that hatching nearly ceased immediately eggs were exposed to *c.* 100% R.H. and recommenced as soon as they were returned to dry air.

Figure 1 also shows that although all eggs were maintained at 37°C at 54% R.H. for a further 9 hr after the conclusion of the experiment only a few more eggs hatched, indicating that many of the eggs which had been prevented from hatching were dead. There was a mortality of 27% in one group as against 7% in the control (Fig. 1(*a*)) and of 66% in the other as against 1% in the control (Fig. 1(*b*)). The magnitude of the mortality was related to the total time of exposure of each group to a high humidity.

Thus, most of the eggs of *D. ovis* which were commencing to hatch or in the process of hatching were prevented from hatching as soon as they were exposed to a high humidity, and many were killed subsequently by an exposure as short as 3 hr.

(iii) *Estimation of the Mortality of Eggs Caused by Prevention of Hatching by High Humidities.*—If it is assumed that eggs hatch at a constant rate during a time *T*,

then, as hatching ceases as soon as eggs are exposed to high humidities, the percentage of eggs which fail to hatch and die is $(t/T) \times 100$, where t is the length of time the eggs are exposed to a high humidity during T the time under consideration. Therefore, $(t/T) \times 100$ is the anticipated percentage mortality of the eggs. To test whether this method was valid the following experiment was performed.

Eggs which were expected to hatch within 24 hr were divided into four groups. All groups were kept at 37°C at 54% R.H. and examined at hourly intervals until eggs commenced to hatch, when three of the groups were exposed to 37°C at *c.* 90% R.H. The R.H. of the air around the eggs became *c.* 90% within 2 min. The fourth group was left at 37°C at 54% R.H. as a control. One group was removed from

TABLE 3
ACTUAL AND PREDICTED MORTALITY OF HATCHING EGGS OF D. OVIS EXPOSED TO 90% R.H.

Treatment	No. of Eggs	Mortality (%)	
		Actual	Predicted
22 hr at 54% R.H.	92	7	0
4½ hr at 90% R.H. followed by 17½ hr at 54% R.H.	91	24	23
9 hr at 90% R.H. followed by 13 hr at 54% R.H.	90	49	41
22 hr at 90% R.H.	94	93	100

90% R.H. after 4½ hr and another after 9 hr, and both were returned to 37°C at 54% R.H. After 22 hr all groups were examined and the number of eggs which had failed to hatch counted. The eggs were returned to 37°C at 54% R.H. for another 6 hr during which time no more eggs hatched. Thus the eggs which had failed to hatch were dead. Table 3 shows the reasonable agreement between the actual and predicted percentage mortality of eggs.

If on exposure to a high humidity there is a delay before the R.H. of the air immediately surrounding all of the eggs will prevent hatching, the percentage of eggs which will not hatch and die is $\{(t-t')/T\} \times 100$, where t' is the time taken for the air to reach a R.H. which will prevent hatching.

An experiment was carried out in which eggs which were within 24 hr of hatching were mounted between a cover-glass and filter paper. The mounts were held together in bundles of 10 and exposed to 37°C at a R.H. of 95–100%. Cobalt thiocyanate papers included in the mounts showed that the R.H. of the air within all the mounts in a bundle was over 90% R.H. within 2–4 hr.

Mounts with eggs which were commencing to hatch were divided into five groups of 10 and formed into bundles. Three bundles were exposed to 95–100% R.H. for either 3, 6, or 12 hr before being exposed to 54% R.H., one to 95–100% R.H. for 24 hr, and another to 54% R.H. for the entire 24 hr. At the end of 24 hr the number of eggs which had not hatched was determined and all unhatched eggs were exposed to 54% R.H. for 6 hr to check whether they were still alive, but none hatched. The experiment was repeated twice. The number of eggs in each mount differed slightly, and as the R.H. became stabilized in the outermost mounts in a bundle first, there was a slight variation in the rate at which the eggs became exposed to the high humidity. Even so, Table 4 shows that there was good agreement between the actual and predicted mortalities.

TABLE 4

PERCENTAGE MORTALITY OF HATCHING EGGS OF D. OVIS WHEN EXPOSED TO A RELATIVE HUMIDITY > 90% FOR 3, 6, 12, AND 24 HR AND WHEN THE RELATIVE HUMIDITY REQUIRED 2–4 HR TO BECOME STABLE

Expt. No.	Exposed to 54% R.H. for 24 Hr		Exposed to 90% R.H. before being Exposed to 54% R.H.							
			3-Hr Exposure to 90% R.H.		6-Hr Exposure to 90% R.H.		12-Hr Exposure to 90% R.H.		24-Hr Exposure to 90% R.H.	
	No. of Eggs	Mortality (%)	No. of Eggs	Mortality (%)	No. of Eggs	Mortality (%)	No. of Eggs	Mortality (%)	No. of Eggs	Mortality (%)
I	54	0	55	7	54	4·8	54	48·1	54	72·2
II	57	0	57	8·8	57	15·8	57	36·8	57	89·5
III	99	4	100	10	100	12	100	35	100	80
Total	210	1·9	212	7·5	211	13·7	211	38·9	211	80·6
Expected mortality (%)		0		0 – 4·2		8·3 – 16·7		33·3 – 41·7		83·3 – 91·7

(c) *Effect of Exposure to Free Moisture*

(i) *Nymphs and Adults.*—Separate collections of females, males, and nymphs were each divided into seven groups which were submerged in water at 37°C for 1–7 hr. When the lice were removed from the water, the excess moisture was wiped from their bodies and half of each group was exposed to 37°C at *c.* 40% R.H., and half to 37°C at 90% R.H. for 6 hr before being exposed to *c.* 40% R.H. After 24 hr the numbers of living and dead lice were determined. Figure 2 shows that subsequent exposure to 90% R.H. for 6 hr reduced the time of submersion required to kill the lice. This experiment was repeated twice with similar results, and in all *c.* 100 males, 70 females, and 300 nymphs were exposed to each experimental condition. There was a slight variation in the time required to kill the lice in the experiments. It was

found that immersion for 4–6 hr in water is required to kill most nymphal and adult *D. ovis* if they are kept at a low R.H. after submersion, but only 2–4 hr if, after submersion, the lice are exposed to 90% R.H. There were no obvious differences between the rates of mortality of each nymphal stage.

Other groups were submerged in water for 1 hr only and then exposed to 90% R.H. for $2\frac{1}{2}$, $7\frac{1}{2}$, or 24 hr before being placed at *c.* 40% R.H. The experiment was repeated twice with similar results and at least 58 males, 94 females, and 153 nymphs were exposed to each experimental condition. No mortality was caused by the $2\frac{1}{2}$-hr exposure, *c.* 50% were killed by the $7\frac{1}{2}$-hr exposure, and all were dead after 24 hr.

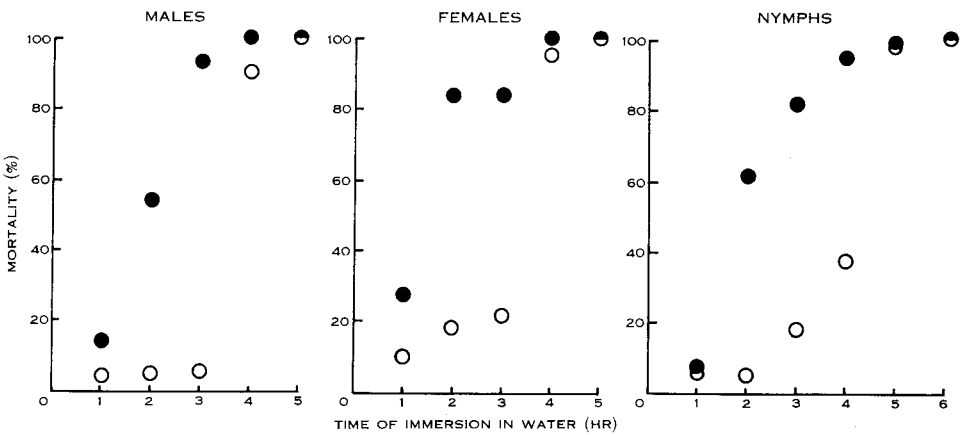

Fig. 2.—Mortality (%) of *D. ovis* after various periods of immersion in water: O placed in air at *c.* 40% R.H. immediately after removal from water; ● after removal from water placed in air at 90% R.H. for 6 hr before being placed in air at *c.* 40% R.H.

Groups of 100–200 nymphs and adults were placed on different types of wool from sheep, and both lice and wool were submerged in water for various periods. Afterwards the excess moisture was removed and they were exposed to *c.* 40% R.H. Again 4–6 hr were required to kill nymphs and adults.

(ii) *Eggs.*—Eggs, which were laid by females in the laboratory and were less than 36 hr old, were divided into groups and immersed in water at 37°C for 1–9 days. The experiment was carried out in stages and on each occasion some eggs were not immersed in water but were incubated at 37°C and 54% R.H. as a control. After immersion in water the eggs were incubated at 37°C at 54% R.H. Table 5 shows that an immersion of 7 days was required before there was an appreciable reduction in the percentage of eggs that subsequently hatched. The embryos within more than 75% of the unhatched eggs which had been immersed 7–9 days were nearly fully developed.

(*d*) *Effect on Lice and Eggs of Soaking the Fleece of Infested Sheep*

Four infested sheep with fleeces *c.* 3 in. long were dipped individually in a bath of water. The sheep were submerged and the fleece was thoroughly soaked. Afterwards they were placed in a covered pen to delay drying. Two of the sheep were redipped and soaked again 2 hr later. The sheep were examined 24 hr later, and the

fleeces were still wet. The number of living and dead lice was then determined by visual examination of 10 areas each 3 in. square. Many dead and only a few living lice were seen. Two days after dipping, samples of fleece a ½ in. square were dry-

TABLE 5
EFFECT OF IMMERSION IN WATER ON THE PERCENTAGE HATCH OF EGGS OF D. OVIS*

Time of Immersion (in days):									
0	1	2	3	4	5	6	7	8	9
Percentage Hatch									
100	66								
84	73	83	71						
84		93	90	60					
89			84	68	67				
63			82	58	53	40			
76						64	10	0	0
66						64	34	2	0
69						61	26	0	4†

* Average number of eggs in each experiment 50, range 38–73.
† 27 eggs.

shaved from the skin. The number of living and newly dead lice was determined. The mortality which had occurred was similar in each sample and Table 6 shows that over 75% of the louse population in the areas sampled had been killed.

TABLE 6
EFFECT OF SOAKING THE FLEECE OF SHEEP ON THE NUMBER OF D. OVIS

No. of Samples	Mean No. of Lice per Sample	Total No. of Lice	Living			Dead			Mortality (%)	Mean No. of Survivors per Sample
			♂	♀	Nymphs	♂	♀	Nymphs		
20	6·95	139	2		1	86		50	98	0·15
10	20·1	201	1	0	20	30	28	132	89	2·1
10	19·7	197	3	8	36	32	40	78	76	4·7
4	77·8	311	3	5	45	20	35	203	83	13·25

Eggs were removed from three sheep, and those which were less than 5 days old were incubated at 37°C at 54% R.H. The number of eggs which hatched subsequently were 18 of 21, 55 of 69, and 37 of 54.

IV. Discussion

Immersion in water for 4–6 hr killed most nymphal and adult *D. ovis* and if drying was delayed by exposure of over 7½ hr to 90% R.H., an immersion of even 1 hr could be lethal to over 50%. Eggs, however, required immersion for 7 days to produce an appreciable mortality. Relative humidities of over 90% were lethal only to eggs, specifically at the time of hatching, and it was possible to predict with reasonable accuracy the mortality which would ensue from such an exposure. Female *D. ovis* lay only one egg every 1–2 days (Scott 1952), and consequently the number of eggs which hatch each day may be expected to be relatively constant compared with insects which lay a large number of eggs in a short time. The eggs of *D. ovis* take 10 days to develop and hatch (Scott 1952; Murray 1960), so *c.* 10% of eggs may be expected to hatch daily. Consequently, should high humidities be maintained near the skin of a sheep for 1 day, a 10% mortality of all the eggs present in that region could be expected. Thus, should a rainstorm thoroughly soak the fleece and the fleece remain wet near the skin, there may be not only a direct mortality of 75–100% nymphs and adults, but also a 10% mortality of eggs each day a R.H. of over 90% persists near the skin.

Four types of factors determine the severity of the effects of rain on populations of *D. ovis*. Firstly, the length, density, and greasiness of the fleece influence the ease with which it may be wetted and the rapidity with which it may dry subsequently. The length of the fleece is probably the most important of these factors because the shorter the fleece the quicker it will dry. A long fleece, particularly if dense, does not become soaked readily, but once saturated with water it may take a few days to dry. A greasy fleece does not become soaked easily, and consequently the lice on these sheep may not be killed. Secondly, heavy rainfall, such as is frequently associated with thunderstorms, is required to soak a fleece but the rain may fall unevenly even within one paddock, and thus may produce an erratic effect. The behaviour of the sheep is a third variable, because some sheep may find shelter during a thunderstorm. Finally, the severity of the effect of rain is influenced by the distribution and the size of the louse population on the sheep when the fleece is soaked. The lice on the underparts of the sheep are less likely to be killed than those on the back and sides, and more survivors may be expected from a large population, particularly from the many eggs present.

The number of *D. ovis* on sheep usually declines after shearing and during the summer, and increases during the winter (Scott 1952). The size of the louse populations on the sheep under observation declined during the summer as expected, and consequently when the rain soaked the fleeces in the autumn the numbers of lice were low. The resultant effect was so severe that the populations failed to recover during the winter. It would appear therefore that populations of *D. ovis* must be of a certain size at the commencement of winter if the usual increase in numbers is to occur, and this size appears to be equivalent to about a grade 2 infestation. Thus the severity of adverse factors operating upon a population of *D. ovis* in the summer and autumn can determine the number of lice present several months later at the end of the subsequent winter.

V. Acknowledgment

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