THE ECOLOGY OF LICE ON SHEEP

IV. THE ESTABLISHMENT AND MAINTENANCE OF POPULATIONS OF LINOGNATHUS OVILLUS (NEUMANN)

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Summary

Linognathus ovillus has been found on all regions of the sheep except the lower aspects of the limbs, but populations are maintained throughout the year only on the parts of the body covered with hair, particularly the face. The inability of *L. ovillus* to multiply below a constant temperature of 30°C, or to survive prolonged exposure to cold temperatures, probably prevents maintenance of populations on the lower parts of the legs.

Only adult lice were transferred from sheep to sheep, and fewer were required to establish a population on the hairy face than on the parts of the body covered with wool. The greasiness and length of the wool caused females to lay eggs less densely, required a greater density of males and females for fertilization, and resulted in a greater mortality of nymphal and adult lice.

Lice disperse continually from the face into the surrounding wool, and the consequent density of lice in this wool frequently becomes sufficient for the population to maintain itself, thus resulting in a swarm of lice in that area.

Shearing removes few lice from the parts of the body covered with hair, but many from those parts covered with wool. Thus, whereas the density of lice on the face is little affected by shearing, that on the body is reduced considerably. When a sheep is exposed to atmospheric temperatures of *c.* 28°C the temperature next to the skin rises to over 38·5°C. Few eggs develop and hatch at this temperature. These two factors probably account for the disappearance of *L. ovillus* from the body after shearing in the spring, and during the following summer. The occurrence of lethal temperatures within the fleece during the summer may also be a contributory factor.

Observation of an infested flock over a period of a year showed that the sheep which were most heavily infested in the autumn were also the most heavily infested in the subsequent spring. This indicates that the size of a louse population on a sheep in the spring may frequently be directly dependent on its size at the commencement of the previous winter.

I. INTRODUCTION

Linognathus ovillus (Neumann), the face louse of sheep, and *L. pedalis* (Osborne), the foot louse, infest the parts of the body of sheep which are covered with hair. Their numbers increase during the winter, and by spring swarms of lice may be found in the wool surrounding the predilection sites. Murray (1955) suggested that this characteristic feature of linognathid infestations of sheep may be due to factors associated with the integumental covering which is sharply delineated into hair and wool. Subsequent observations have shown that the behaviour of these two species on sheep is different (Murray 1963). *L. pedalis* congregates into clusters and most lice are found on the hair-covered parts of the legs. *L. ovillus*, on the other hand,

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continually disperses and, in heavy infestations, the greatest numbers are found in the wool surrounding the face (Plate 1, Fig. 1).

It appeared therefore that the dispersal and thus the ecology of *L. ovillus* could be influenced by the nature of the integumental coverings, and the manner in which the hair and wool coats of sheep influence the distribution and numbers of *L. ovillus* is reported in this paper.

Only new techniques are described, as the others used were described previously (Murray 1957*a*, 1957*b*, 1960).

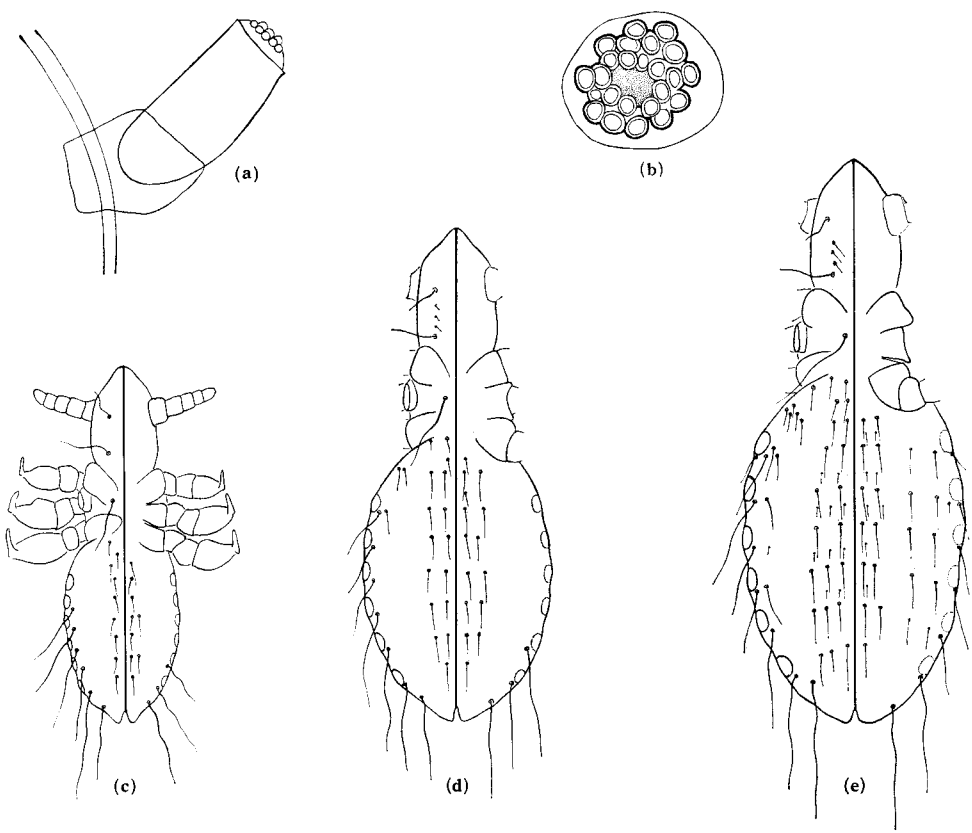

Fig. 1.—Distribution of the setae on dorsal and ventral aspects of the nymphs of *Linognathus ovillus*: (*a*) egg; (*b*) cap of egg; (*c*) stage I nymph; (*d*) stage II nymph; (*e*) stage III nymph.

II. Biology of L. ovillus

(*a*) *Life Cycle*

L. ovillus is a blood-sucking louse. Its life cycle is completed in 5 weeks, the stages being the egg, three nymphal instars, and the adult male and female (Murray 1955). The egg is dark in colour with a micropyle of characteristic structure on its cap (Figs. 1(*a*), 1(*b*)). The nymphal stages may be identified by their size and the distribu-

tion of the abdominal setae (Figs. 1(*c*), 1(*d*), 1(*e*)). The males are smaller than the females and the genital apparatus and appendages of both sexes are easily seen. Detailed descriptions of the adults have been given by Ferris (1932).

(*b*) *Transmission*

L. ovillus may be seen on the tip of the hair or wool of the heavily infested regions on the sheep, particularly on warm days or when the sheep is standing in the sun, and lice are transferred when these regions brush against another part of the body or against another sheep (Murray 1955).

TABLE 1
NUMBER OF L. OVILLUS WHICH TRANSFERRED TO A CLOTH OR PAPER TISSUE HELD AT THE HAIR AND FLEECE TIP OF THE FACE OF A SHEEP FOR 1 MIN

Size of Population on Face of Sheep	Number of Lice Transferred				
	Total	Males	Females		Nymphs
			Unengorged	Engorged	
c. 20	0	—	—	—	—
c. 20	0	—	—	—	—
20+	0	—	—	—	—
150+	0	—	—	—	—
150+	0	—	—	—	—
150+	1	—	1	—	—
150+	1	—	—	1	—
150+	1	1	—	—	—
150+	1	—	—	1	—
200+	4	1	1	2	—
c. 500	10	3	5	2	—
c. 500	8	4	2	2	—
500+	25	1	18	6	—
500+	43	7	34	2	—
500+	74	21	50	3	—
1000+	168	23	131	14	—

The visible lice on the wool tip of a heavily infested sheep were removed and the stages present identified. All of 712 lice removed were adults; 87 were males and 625 were females. Two types of females were distinguishable, those which were plump, bluish, and appeared to be engorged with blood and those which were thinner, brownish, and not engorged. There were 125 engorged and 500 unengorged females.

It was found that the warmth of a hand placed on the face of an infested sheep was sufficient to attract lice to the tip of the hair even when the atmospheric temperature was 5°C. Cloths or paper tissues were held with the hand on the tip of the hair or wool of the face region for 1 min when the atmospheric temperature was 10–15°C. Only adults, males and females, transferred to the cloth or tissue, and in greater numbers when the population was more dense (Table 1).

Sheep were placed in a cool room at an air temperature of 10°C. No lice were visible on their faces at this temperature, but many adults moved to the hair tip and became visible within 1 min whenever the sheep were removed from the cool room to an atmospheric temperature of 24°C.

(c) *Oviposition*

(i) *Number of Eggs Laid by Engorged and Unengorged Females.*—Engorged and unengorged females were collected and divided into groups of 25–30 lice. Each group was placed in a glass tube with nylon fibres for egg attachment, and exposed to 35°C at 54% R.H. The numbers of lice which survived after 24 and 48 hr and the

TABLE 2
SURVIVAL AND EGG PRODUCTION OF ENGORGED AND UNENGORGED FEMALE L. OVILLUS AFTER EXPOSURE FOR 24 AND 48 HR TO 35°C AT 54% R.H.

	No. of Females	After 24 Hr		After 48 Hr	
		No. of Dead Females	No. of Eggs Laid	No. of Dead Females	No. of Eggs Laid
Engorged female	25	5	21	22	24
	30	1	24	25	30
	28	2	21	22	24
	30	0	24	25	29
	29	2	22	26	29
Totals	142	10	112	120	136
Unengorged female	30	8	1	30	1
	29	6	2	29	2
	30	9	1	30	1
	30	7	0	30	0
	29	5	2	29	2
Totals	148	35	6	148	6

number of eggs which had been laid were counted. Most eggs were laid within 24 hr, but whereas 112 eggs were laid by 142 engorged females, only six eggs were laid by 148 unengorged females during this period (Table 2). Furthermore, the unengorged females died more rapidly than the engorged females.

A collection of 134 females was made and the engorged and unengorged females separated into two groups. Both groups were placed in glass tubes with nylon fibres and exposed to 35°C at 54% R.H. for 24 hr. Only four eggs were laid by the 106 unengorged females, whereas 27 eggs were laid by the 28 which were engorged. Forty of the unengorged females died whereas none of the engorged lice died.

The surviving unengorged females were divided into two groups, one of which was returned to 35°C at 54% R.H. All of the 31 lice in this group died during the

next 24 hr without laying any eggs. The other group of 35 females was placed on the face of a louse-free sheep, and the following day 10 eggs were found and 25 females, which were now engorged, were recovered. These were then exposed to 35°C at 54% R.H. and 24 hr later they had laid six eggs. Thus, 16 eggs were laid in 48 hr by the 35 unengorged lice after they had been allowed to feed.

(ii) *Oviposition Behaviour.*—Female lice* together with glass wool were placed in cells along which a temperature gradient of 20–40°C was established. Their behaviour at the time of oviposition was similar to that of *L. stenopsis* (Burm.) and *L. pedalis* (Murray 1957*a*, 1960). Initially they moved to the warm end where they rested with their heads directed towards the warm end, and then they turned about, grasped a fibre with their gonopods, and laid an egg. Consequently, all of the 35 eggs laid were deposited at the warm end of the cell with their end of attachment towards the warm end. Other lice in similar cells, but exposed to a constant temperature of 35°C, attached their eggs to the glass wool throughout the cell with the end of attachment directed towards either end.

(iii) *Influence of the Diameter of Fibre on the Number of Eggs Laid.*—The eggs of *L. ovillus* may be found attached either to the hair or the wool of sheep.

Four groups of 100 females were placed in chambers which allowed them the choice of coarse or fine nylon fibres for egg-attachment. The numbers of eggs laid were 34, 32, 72, and 30 on the coarse fibres and 17, 30, 27, and 29 on the thin fibres respectively. Thus, when given a choice, females attached eggs readily to both coarse and fine fibres.

Engorged females were divided into two groups and placed at 35°C and 54% R.H. One group was given nylon fibres similar in diameter to hair from the face, and the other glass wool the diameter of which was similar to fleece wool. After 24 hr, 89 females had laid 90 eggs on the coarse nylon fibres, and on the fine glass wool 83 females had laid 78 eggs. Thus when not allowed a choice the females laid similar numbers of eggs on coarse and fine fibres.

(iv) *Influence of Temperature and Humidity on the Number of Eggs Laid.*—Female lice were divided into groups of 20–30 which were placed in glass tubes with nylon fibres. Five groups were exposed to each of the following temperatures: 20, 25, 30, 35, or 40°C, and one group of each lot of five was exposed to 33, 54, 75, 90, and 100% R.H. After 24 hr the number of eggs laid was counted. This was repeated twice so that a total of at least 60 lice was exposed to each combination of temperature and humidity. The results of each experiment were similar. Figure 2 shows that most eggs were laid at 35°C, and few or none were laid at 25 and 20°C. Humidity had no great influence on the number of eggs laid.

(*d*) *Development of Eggs*

(i) *Influence of Type of Fibre.*—Female lice were removed from a heavily infested sheep and kept at 35°C and 54% R.H. Fleece wool, hair from the face, glass wool, and nylon were provided. The eggs which were laid and attached to these materials

* In this and in all subsequent experiments only engorged females were used.

within 24 hr, and others which became detached, were exposed to 35°C at 54% R.H. All eggs developed and hatched satisfactorily.

(ii) *Influence of Temperature and Humidity.*—Lice were exposed to 35°C at 54% R.H. with nylon fibres, and after 24 hr the eggs which were laid were removed. These eggs were exposed to various temperatures and humidities for 3 weeks to allow sufficient time for those at the lower temperatures to hatch. The numbers of eggs which had hatched and the numbers of unhatched eggs in which there was a well-developed embryo were then determined. Half of the unhatched eggs of each group were then placed at 35°C and 54% R.H. to determine whether they were dead.

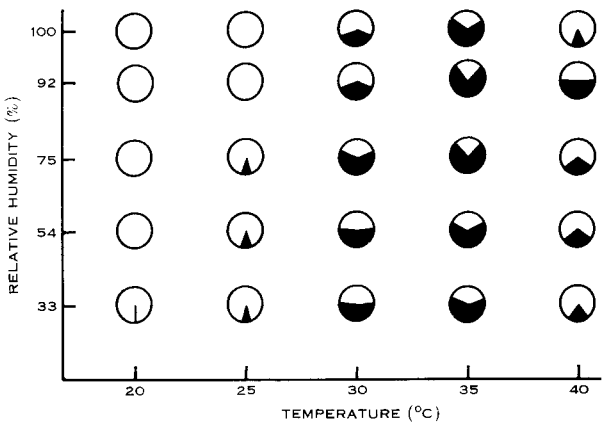

Fig. 2.—Influence of temperature and humidity on oviposition of *L. ovillus*. The shaded area represents the percentage number of eggs laid.

It was not possible to collect sufficient eggs at any one time to expose them simultaneously to all combinations of temperature and humidity desired. The experiment was therefore carried out in stages and some eggs from each collection were exposed to 35°C at 54% R.H. as a control. The remainder were divided into groups, usually of equal numbers, and were exposed to 27, 30, 32, 35, 37, 38·5, and 40°C. At each temperature a group was exposed to 33, 54, 75, 92, and 100% R.H. At least 50 eggs were exposed to each combination of temperature and humidity.

In 12 of the 16 control groups, 85–100% of the eggs hatched and in the remaining four, 71, 76, 81, and 82% hatched. In experiments where the lower percentage hatch of eggs occurred in the controls, eggs had been exposed to the same combinations of temperature and humidity three times, and on each of the two other occasions 85–100% of the controls had hatched. However, the results obtained in each of the experimental groups were similar on all three occasions, and therefore could be summed.

Figure 3 shows that most eggs hatched from 32–37°C at 33, 54, and 75% R.H. Morphogenesis proceeded to an advanced stage at temperatures between 30 and 38·5°C except at 100% R.H. at 30, 32, and 38·5°C (Fig. 4). All unhatched eggs were

found to be dead. In another experiment, 41 eggs were exposed to 35°C at 7% R.H. and 78% of them developed and hatched.

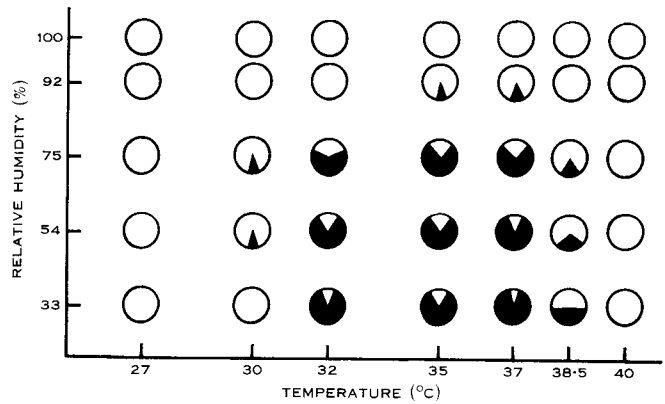

Fig. 3.—Percentage hatch of eggs of *L. ovillus* maintained at constant temperatures and humidities. The shaded area represents the percentage hatch of eggs.

(e) *Dispersal of Nymphs*

Areas, 3½ in. square were marked on the sides of Merino sheep and the wool was clipped to a length of ¼–½ in. Each 3½ in. square was divided into 49 half-inch squares, and nymphs were placed in the central square. For 3–5 days their dispersal and the stage of their development was recorded daily, and thereafter every 2–3 days until only adults were present.

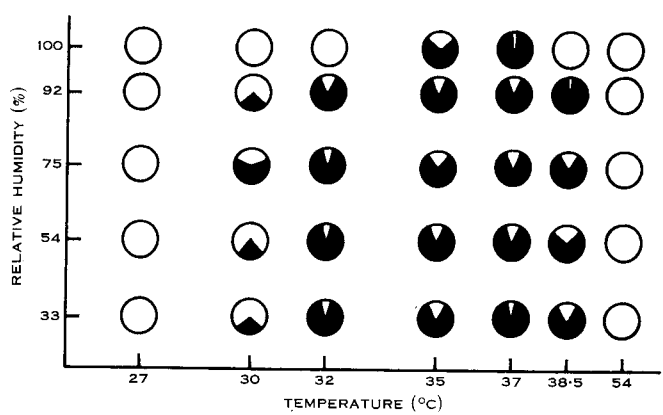

Fig. 4.—Influence of constant temperatures and humidities on morphogenesis of eggs of *L. ovillus*. The shaded area represents the percentage number of eggs in which the embryo reached an advanced stage of development.

Stage I nymphs were obtained from eggs hatched in the laboratory, and about 50 were placed in the central square of three experimental areas on three different

sheep. Some nymphs died, but the presence of nymphs in increasing numbers in the peripheral squares showed that there was also a continual dispersal; 14–16 days later three adults were found scattered over one area, and only one adult on each of the other two areas. A similar number of stage II nymphs was placed in the central square of five other $3\frac{1}{2}$ in. square areas on the body. Again the lice dispersed steadily from the areas, and only 4 (4 ♀), 4 (3 ♂, 1 ♀), 5 (2 ♂, 3 ♀), 6 (3 ♂, 3 ♀), and 8 (3 ♂, 5 ♀) adults were found 8–11 days later. When 100 stage II nymphs were placed in the experimental area, 31 (14 ♂, 17 ♀) adults were found 7 days later. The experiment

TABLE 3
NUMBER OF EGGS LAID BY POPULATIONS OF DIFFERENT DENSITIES OF L. OVILLUS ON THE BODY AND FACE OF SHEEP

Position on Sheep	Surface Area of Experimental Region (sq in)	Nymphal Stage	No. of Nymphs in Initial Infestation	No. of Resultant Adults	No. of Eggs Laid
Body	12·25	I	50	1 (1 ♀)	0
			50	1 (1 ♀)	0
		II	45	6 (3 ♂, 3 ♀)	5
			45	4 (4 ♀)	0
			50	5 (2 ♂, 3 ♀)	10
			50	8 (3 ♂, 5 ♀)	0
			50	4 (3 ♂, 1 ♀)	0
			100	31 (14 ♂, 17 ♀)	33
		III	38	10 (3 ♂, 7 ♀)	8
			38	4 (4 ♀)	0
			50	6 (6 ♀)	0
			50	4 (4 ♀)	0
Face	50	II	60	9 (1 ♂, 8 ♀)	34
			60	5 (1 ♂, 4 ♀)	12

was repeated on four other occasions with 38–50 stage III nymphs. These also dispersed and only 10 (3 ♂, 7 ♀), 4 (4 ♀), 6 (6 ♀), and 4 (4 ♀) adults were found 6–7 days later. Nymphs placed on the face dispersed similarly.

There was a steady loss of nymphs due to dispersal and to death, with the result that there was a decrease in the density of each subsequent stage and few adults developed (Table 3). No stage was observed to congregate together to form clusters, and consequently the density of each stage was dependent on the density of the preceding stage.

(*f*) *Survival at High Temperatures*

A group of 10 male, 21 female, and 58 nymphal lice were exposed to 47–48°C at 75% R.H. All were dead within 1 hr.

III. Influence of some Components of the Environment on the Establishment and Maintenance of Populations of L. ovillus

(*a*) *Type of Hair and Wool Covering of the Sheep*

(i) *Effect on Oviposition.*—Previous observations on females on the hairy face of sheep showed that the female lays an egg a day, which is usually attached to the hair *c.* 0·1 in. from the skin with its end of attachment nearest to the skin. After laying each egg the female usually moves only 0·1–0·2 in., so that she frequently becomes surrounded by a cluster of eggs. However, as a rule, females change their position every few days and do not lay all their eggs in one vicinity (Murray 1955).

Areas 6 in. square were marked on the face and on the sides of Merino sheep, the fleece of which was 1–1½ in. long. These areas were divided into 36 areas each 1 in. square. Sixty females were placed in the centre of each region and their subsequent spread and mortality were determined 6–7 days later when the hair or wool from each 1 in. square was removed from the skin by dry shaving. The wool or hair was soaked in xylol and examined to determine the number and distribution of the eggs laid. Similar results were obtained in each of four experiments. On both the face and body the majority of the lice dispersed from the experimental area or died. Most eggs were laid on the face, their distribution was more restricted, and consequently their density was greater (Fig. 5).

Females placed on the face moved directly down the hair fibre to the skin, whereas many of those placed on the fleece did not move towards the skin for an hour. Frequently they wandered across the tip of the fleece before they travelled directly, or transversely across the fibres, to the skin. Their behaviour was similar even when the fleece was clipped to *c.* ¼ in. and the density of the wool fibres reduced to about one-quarter of their original density.

Two areas were prepared on a greasy-woolled Border Leicester ewe. The wool length on one was ½ in. and on the other 3 in. Fifty females were placed on the tip of the wool of each area, and 10 days later the number and distribution of eggs which had been laid were determined. Figure 6 shows that 136 eggs were laid on the short wool, whereas only 18 were laid on the long wool. The movement of the lice was greatly impeded by grease in the long wool, where many lice became immobilized and died before reaching the skin.

After the fleece was scoured with ether and warm water to remove excess quantities of grease and suint, lice behaved as on the face, and moved down the wool fibres to the skin shortly after they had been placed on the sheep.

The wool covering two areas was scoured with ether and warm water. The length of the wool was ½ in. on one area and 2½ in. on the other. Fifty females were placed on the tip of the wool in the centre of each area, and 4 days later the number and distribution of eggs which had been laid were determined. Figure 6 shows that 79 were laid on the scoured short wool whereas only 30 were laid on the scoured long wool. The eggs laid on the long wool were more scattered.

(ii) *Effect on Number of Females Fertilized.*—Table 3 shows that in three instances the resultant adults from the dispersal experiments with stage III nymphs were all females. They were examined daily for a week and at each examination they were

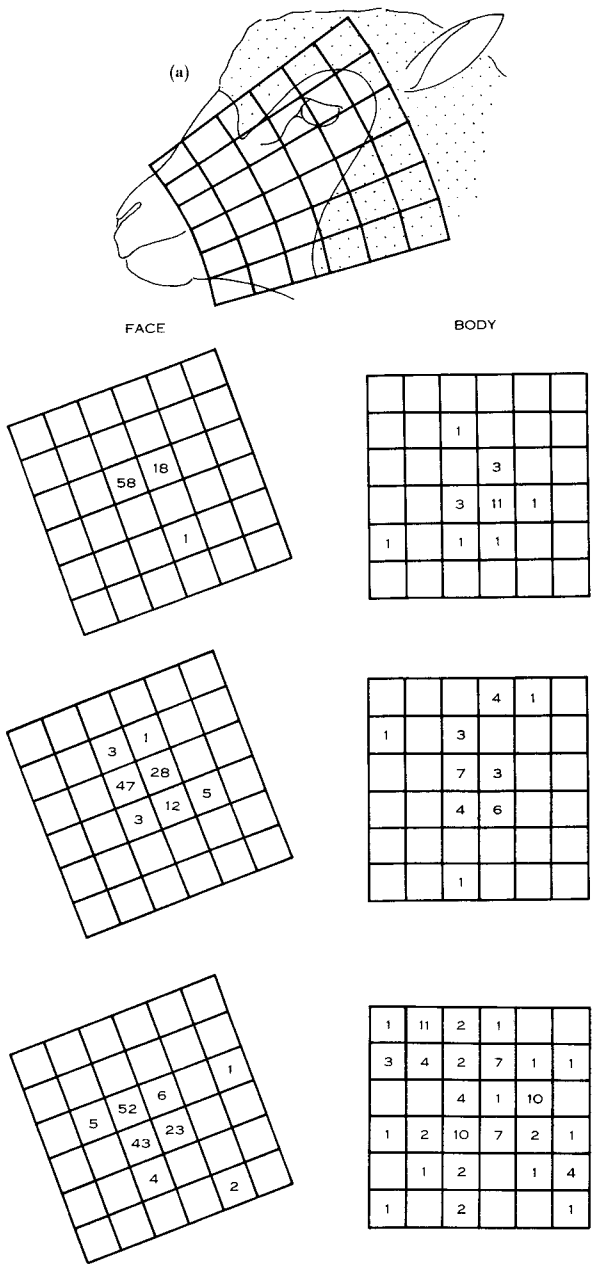

Fig. 5.—Distribution of the eggs laid by female *L. ovillus* on areas 6 in. square on the face and body of sheep. (*a*) The approximate position of the area on the face of a sheep.

brown in colour and appeared to be unengorged. The wool was then removed and examined in xylol for the presence of eggs, but none was found.

Six unfertilized females obtained from stage I and II nymphs (Table 3) were placed in the central square of a $3\frac{1}{2}$ in. square area. Thirty-four males were distributed throughout the area by placing two in the central square, two in each of the neighbouring squares, and one in each of the surrounding squares. Three females commenced to lay eggs within a week and became engorged in appearance. Thus at this density of males not all females were fertilized.

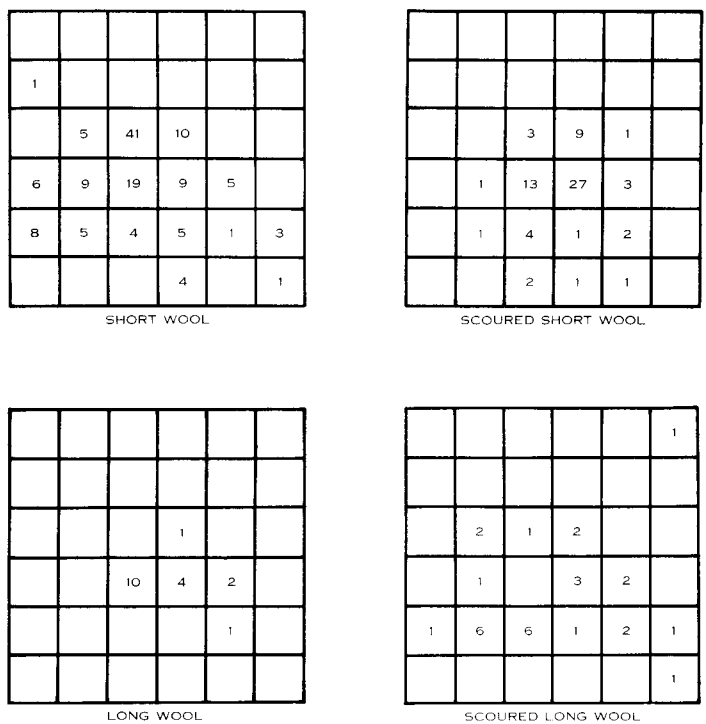

Fig. 6.—Distribution of the eggs laid by female *L. ovillus* on areas 6 in. square on the body of sheep.

On the other areas where there were both males and females, not all of the females were fertilized. Those which were fertilized commenced to lay eggs within a week and appeared engorged. Examination of the eggs at the end of the experiment showed that morphogenesis was proceeding normally within the eggs. The distribution of the eggs which were laid in the areas on the bodies of the sheep in these experiments was scattered, as described previously (see Section III(*a*)(i)).

Groups of 60 stage II nymphs were placed on the faces of each of two sheep. They dispersed over the face and 10 days later 9 (1 ♂, 8 ♀) adults were found on one sheep, and 5 (1 ♂, 4 ♀) on the other (Table 3). All but one of these females were laying eggs, and 34 and 12 eggs were found respectively. These populations became established and were still present on the sheep 4 months later.

In summary, the experiments on nymphal dispersal provided adult populations on the body of greater densities of males and females than those which maintained a population on the face, but many of the females did not become fertilized and fewer eggs were laid. It would appear from these results that at similar densities more females became fertilized on the face than on the body.

(*b*) *Influence of the Size of Area on the Face Covered with Hair*

There is a considerable variation in the area covered by hair on the face of sheep. On some sheep, wool fibres of *c.* 1 in. in length are abundant in the region where hair is usually found. These sheep are commonly referred to as being woolly-faced, and none of this type has been found to be even moderately infested with *L. ovillus*.

TABLE 4
INCREASE IN THE NUMBER OF L. OVILLUS ON SHEEP DURING THE WINTER

Sheep No.	23.iii.61	5.vii.61	14.ix.61	Sheep No.	23.iii.61	5.vii.61	14.ix.61
1	56 (16)*	150+	500+	14	3 (3)	0	2–10
2	46 (18)	50+	200+	15	3 (1)	10	0
3	29 (10)	50+	200	16	3 (3)	10†	150
4	77 (15)	20+	100+	17	3 (3)	0	0
5	50 (15)	80+	200	18	4 (2)	8	50
6	50 (15)	100+	500	19	3 (1)	40† (30)	100
7	50 (15)	150+	300	20	2 (2)	5 (3)	2–10+
8	60+ (14)	50+	50	21	4 (4)	20† (15)	200
9	50 (15)	8	2–10+	22	1 (1)	0	0
10	14 (4)	0	2–10+	23	1 (0)	2	0
11	9 (8)	2 (2)	0	24	1 (1)	0	0
12	14 (6)	0	0	25	1 (1)	10+†	50–100
13	2 (2)	4	2–10				

* Number of engorged females in brackets. † Many eggs present.

The faces of four woolly-faced sheep were shorn and *L. ovillus* transferred to them in numbers which would establish an infestation on a hairy-faced sheep. The distribution of the lice was examined regularly as the wool regrew. The number of lice declined and they eventually became restricted to the hair around the mouth before the infestations disappeared. It would appear that a certain area of hair covering on the face of sheep is necessary to maintain a population, otherwise too many lice are lost by dispersal into the wool.

(*c*) *Removal of Wool by Shearing*

It has been shown previously that within a month of an infested sheep being shorn, the number of lice declines rapidly (Murray 1955). Subsequently lice are only found on the face or upper hairy parts of the legs.

Just before the end of winter the wool was shorn from the bodies of three heavily infested sheep (Table 4, Nos. 1, 6, 7) but not from around the face (Plate 1,

Fig. 2). One month later the number of lice had increased from *c.* 500 to *c.* 600, from *c.* 500 to *c.* 600, and from *c.* 300 to *c.* 400 respectively.

Virtually no hair is removed from the face of a sheep by shearing but wool is removed to within $\frac{1}{4}$ in. of the skin, and consequently when the faces of infested sheep were deliberately shorn no lice were removed from the parts of the face covered with hair. Only a few lice were removed with the wool by shearing on cool days but on warm days, or after sheep were placed in a warm atmosphere or after they had stood in the sun, many lice were removed as they had moved from the skin towards the tip of the wool.

(*d*) *Atmospheric Temperature*

It has been observed previously that even on unshorn sheep the number of lice may decline during the spring and summer (Murray 1955). Unshorn sheep with heavy infestations were kept, for the duration of the summer months, in a cold room which maintained an atmospheric temperature of 5–10°C. The numbers of lice were maintained on 3, and increased on 4 of the 7 sheep placed in the cold room.

Three infested sheep were kept in the cold room for several weeks. One day, after their louse populations had been counted, the cooling unit of the room failed for 12 hr during the night. The temperature rose from 10 to 30°C and many lice were visible on the fleece tip when the sheep were examined in the morning. These were being brushed off the faces of the sheep onto the other parts of their bodies and onto the bodies of the other sheep. The temperature of the room was cooled again to 10°C within 3 hr, and 3 hr later the number of lice on the face of each sheep was recounted. On two of the sheep which had a predominantly adult population, the number had fallen from *c.* 200 to *c.* 100, whereas on the third sheep with a predominantly nymphal population there was no appreciable decline.

(*e*) *Effect of the Initial Size of the Population*

Each sheep in a flock of 264 was examined for the presence of *L. ovillus*. All of the 25 sheep found infested were identified by numbered eartags. The number, distribution, and density of the lice on each infested sheep were determined three times during the year, in the autumn (March 23, 1961), in midwinter (July 5, 1961), and a month before they were shorn in the spring (September 14, 1961). Table 4 shows the number of lice found on each sheep at each examination. The louse populations on 7 of the 9 sheep with heaviest infestations at the beginning of winter increased through the year and were still the heaviest in the spring. Of the remaining 16 lightly infested sheep, four developed fairly heavy infestations (Nos. 16, 19, 21, and 25). The whole flock was examined also in September to determine the number of infested sheep and the number of lice on them. An additional 67 sheep were infested but on none was found more than 10 lice. Table 5 shows that the majority of the sheep which were heavily infested in autumn were also the most heavily infested in the spring.

The initial increase in density of lice on all heavily infested sheep occurred along the zone of mergence from hair to wool. Here there were pockets of *c.* 8 females/sq in

which increased to *c.* 20 females/sq in as the population spread along this zone. The position of the greatest density varied between sheep: on some it was around the eye, and on others on the cheek or under the chin. Two features which characterized increasing populations were the presence of many engorged females and numerous eggs. This was striking on sheep Nos. 16, 19, 21, and 25 (Table 4) at the midwinter examination (July 5, 1961) before there was a marked increase in the number of lice.

TABLE 5
COMPARISON BETWEEN INFESTATIONS OF SHEEP WITH L. OVILLUS IN AUTUMN AND SPRING

No. of Sheep Examined	No. of Lice Found in Examination in Autumn	No. of Sheep with Indicated Lice Infestations in Following Spring:					
		0	1–20	21–80	81–160	161–400	400+
240	0	173	67*	—	—	—	—
15	1–20	6	4	3	2	—	—
9	10–80	—	1	1	1	4	2

* On 29 sheep only 1 louse was found and 2–10 lice were found on the remaining 38.

IV. DISCUSSION

L. ovillus is found on all regions of sheep except the extremities such as the lower parts of the limbs, but when their numbers are low they are found principally on the hair-covered parts, particularly on the face. The inability of females to lay eggs below 25°C, of many eggs to develop and hatch at constant temperatures of less than 30°C, and of females to survive more than 4–5 days at 12°C (Murray 1963) may well be part of the explanation for populations failing to become established on the lower parts of the limbs. The oviposition behaviour was similar to that of other lice which have been studied, particularly *L. stenopsis* and *L. pedalis* (Murray 1957, 1960), and like *L. pedalis* the various types of hair fibre found on the sheep did not influence markedly the number of eggs laid. Furthermore, the temperature and humidity requirements for oviposition and egg development were within the range found near the skin on most parts of the body. Thus, the distribution of *L. ovillus* on the body of sheep was not associated with differences between the microclimate near the skin of the parts covered with hair and those covered with wool, nor was it associated with differences between the thickness of hair and wool fibres.

There was no evidence to suggest that *L. ovillus* may reproduce parthenogenetically, so the density of males and females determined the number of fertilized females. Neither nymphs nor adults clustered together as do those of *L. pedalis*, the foot louse of sheep (Murray 1963), and each stage dispersed. Thus the density of males and females in an area depended largely on the density of each preceding stage, and hence to depend on the density of the eggs deposited within the area.

Only adult males, and unfertilized and fertilized females, were transferred from sheep to sheep, and to establish an infestation the fertilized females, which were engorged and did not require a blood meal before they laid an egg, were the most important. Females dispersed more rapidly on the body than on the face, and consequently the resultant density of the eggs laid was less on the body. After the fleece had been scoured with ether and water to remove the grease and suint the lice behaved as they did on the face. Excessive quantities of grease and suint immobilized the lice, and were an important cause of mortality on the body, particularly in long fleeces. The length of the fleece influenced the number and density of eggs laid and, as may be seen in Figures 5 and 6, more eggs were laid when the fleece was short. These two factors, the length and greasiness of the wool, were probably responsible also for the different densities of males and females required to assure fertilization on the face and on the body. Thus, on the parts of the body covered with hair, the behaviour of the females leads to a greater density of eggs, fewer males and females are required to assure fertilization, and the mortality of lice can be less. These reasons explain why *L. ovillus* becomes established on the face rather than on the wool-covered parts of the body. They also offer an explanation for the observed fluctuations in numbers and distribution.

Although 4–8 females were sufficient to maintain a population on the face, i.e. a density of 0·08–0·16 females/sq in, 17 females in 12·25 sq in, i.e. 1·4 females/sq in, was inadequate to establish a population on the body of a Merino (Table 3). Thus if a density D is required to establish and maintain a population on the hair-covered face, a density D^n is required on the wool-covered parts on the body. The value of n is always > 1 and varies from part to part of the body according to the influence of factors such as the grease and suint content, the length, and the microclimate of the fleece. Some of these factors vary seasonally.

Although the lice on the face may appear to be sedentary, they are in fact dispersing over the face and from the face, so a certain area of hair-covering is required or they disperse too rapidly into the wool for a population to be maintained. Their dispersal may be by active movement into the surrounding wool, or passively by being brushed off the face onto other parts of the body. All these lice suffer a similar mortality, but the losses in the wool surrounding the face are replaced by the entry of more lice from the face. In addition, the wool surrounding the face probably presents a barrier which slows the rate of dispersal. These two factors offer an explanation for the observed increase in the density of lice in the wool immediately surrounding the face. Thus it becomes possible for the density in this region to reach the value D^n, after which the population maintains itself. Any factors which reduce the value of n in this region will assist in the establishment of a louse population. Reduction of the wool length over the cheeks, when the sheep are wigged in the autumn, could well be sufficient (Plate 1, Fig. 1).

Once a population becomes established, sufficient lice may disperse from this focus to become established in the neighbouring wool. Should there be several foci these eventually merge and give the appearance of a swarm of lice around the face (Plate 1, Fig. 1). This sequence of events has been observed (Murray 1955, 1963).

With the approach of summer the following factors operate. On warm and sunny days, many lice move to the tip of the fleece where they are brushed off the face, sometimes in sufficient numbers to retard severely the increase in numbers on and around the face. Shearing, the most important factor, removes many from the wool-covered parts of the body, reducing the density to $< D^n$. The parts of the face covered with hair, however, are little affected. During the summer months when the weather is warm the temperature near the skin of the body rises to over 39°C (Murray 1960), at which temperature fewer eggs hatch. Exposure to solar radiation of the intensity encountered in much of Australia can cause the temperatures in most of the fleece covering the dorsal aspects of the sheep to rise rapidly above 47–48°C (Murray 1957*b*) at which *L. ovillus* are killed within an hour. Under these conditions even only partial immobilization by grease could be important, because the lice would be unable to escape from the lethal temperatures. Thus the populations on the wool-covered parts of the body cannot maintain themselves, and they disappear during the summer months. On the face, however, even though fewer eggs may hatch, the density of the louse population is usually still adequate and the lice persist.

The number of lice remaining on the face at the end of the summer largely determines the size of the population at the end of the following winter. If the numbers are small at that time, there will probably be little increase, but if there are many lice on the faces of sheep in the autumn, the number of lice will increase and these sheep will be the most heavily infested at the end of winter.

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ECOLOGY OF LICE ON SHEEP. IV

Fig. 1.—Sheep with heavy infestation of *L. ovillus*. The area of the face which has been wigged is clearly seen.
Fig. 2.—Sheep which were partially shorn. No wool was removed from the head and neck.

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THE ECOLOGY OF LICE ON SHEEP

IV. THE ESTABLISHMENT AND MAINTENANCE OF POPULATIONS OF LINOGNATHUS OVILLUS (NEUMANN)

By M. D. MURRAY

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