THE DISTRIBUTION OF THE EGGS OF MAMMALIAN LICE ON THEIR HOSTS

III. THE DISTRIBUTION OF THE EGGS OF DAMALINIA OVIS (L.) ON THE SHEEP

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Summary

The eggs of *Damalinia ovis* (L.) are attached to the wool and hair fibres of the sheep and have a vertical and lateral distribution, i.e. they may be laid at different distances from the skin and their distribution over the body of the sheep may vary.

The vertical distribution of the newly laid eggs of *D. ovis* is determined by the distance to which the temperature zone suitable for oviposition extends from the skin. This is regulated mainly by skin temperature, skin topography, the depth of the air blanket trapped within the fleece, and atmospheric temperature. Usually the eggs are laid within ¼ in. of the skin.

The factors which influence the lateral distribution are the presence of suitable fibres and temperatures for oviposition. Eggs are not laid on the bare areas of the body because fibres are absent. There are, however, few bare areas on the sheep. The bases of certain hairs on the face, legs, and axilla and inguinal regions are too large in diameter for oviposition but mingled with them are many fibres which are suitable. As there are no areas on the sheep which are entirely covered with hairs of unsuitable diameter for oviposition, fibre diameter has little influence on the lateral distribution of the eggs of *D. ovis*. When sheep are exposed to low atmospheric temperatures, the skin temperature of the extremities falls below that at which *D. ovis* can oviposit. Skin temperature is the main factor which determines the lateral distribution of the eggs of *D. ovis* on the sheep.

I. Introduction

In Part II of this series (Murray 1957*b*) it was shown that the major external stimuli which influenced the oviposition behaviour of *Damalinia ovis* (L.) were the physical features of the environment. The requirements are temperatures between 35 and 40°C, which enable stages 2 and 3 of the behaviour pattern to proceed satisfactorily, and the presence of a fibre of suitable diameter to supply a tactile stimulus just prior to egg laying in stage 3. The absence of either of these necessities can prevent oviposition (Murray 1957*b*).

The eggs of lice are distributed in two ways. They may be laid at different distances from the skin, hereafter referred to as the vertical distribution, and their distribution laterally over the body of the host may also differ.

This paper deals with the influence of variations of temperature and fibre diameter on the distribution of the eggs of *D. ovis* on the sheep.

II. Distribution of the Eggs in the Natural Environment

Several very heavily infested sheep were examined and eggs were found easily on the sides and back where the populations of lice were densest. Elsewhere, eggs

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were also found readily where lice were present, except on the ears and legs, and none was found on the bare areas of the body.

Because the eggs are attached to the wool fibres, they are gradually carried away from the skin as the fibres grow. It was necessary, therefore, to determine their age in order to locate the exact site of oviposition.

(*a*) *Technique for the Examination of a Louse Population*

The wool from areas of *c.* 1 sq. in. was dry-shaved from the skin with a sharp scalpel, care being taken not to disturb the arrangement of the fibres. This gave a neat staple of wool of which only a small vertical section, removed with sharp scissors, was examined at a time. The section of the staple was soaked in xylol and squeezed between two glass slides, the upper one of which was ruled with parallel lines at ¼-in. intervals so that the length of the staple and the position of the eggs could be determined. As xylol has about the same refractive index as wool fibres, the sample was rendered transparent which enabled the lice and eggs to be seen clearly. Furthermore, the living lice and eggs could be distinguished from the dead because the living appeared white and opaque but the dead were transparent. As the embryo could be seen within the egg it was possible to determine its stage of development. In addition, an egg which had hatched could be distinguished from an egg which had died because the egg cap of the dead egg was undisturbed. In some instances it was possible to determine the stage of development at the time of death; not infrequently death occurred during hatching.

When it was inconvenient to examine the material on the day of collection, it was stored in a deep-freeze chamber in which it could be kept in a satisfactory condition for several months.

(*b*) *Results*

The distribution of all recently laid eggs was determined in fleeces of different lengths. All the samples were collected in the winter months from sheep which were kept under cover. The results are presented in Figures 1(*a*) – 1(*e*) from which it may be seen that over 70 per cent. of the recently laid eggs in each sample were laid within ¼ in. of the skin and that, as the fleece became longer, they were found further from the skin.

III. The Influence of Variations in Hair Diameter in the Environment

The principal bare areas on the sheep are under the tail, around the vulva, the lips, inside the ears, and the hoofs. Elsewhere the body is covered with two types of fibres: the wool fibres, which cover most of the body, and the hair fibres which occur on the legs, the face, the axilla, and the inguinal regions. The hair fibres vary considerably in the diameter at their base and tend to taper towards the tip; although many are as fine as wool fibres the diameter of others may be as much as 10 times greater.

A collection of 900 lice was placed in a glass tube with hair from the leg of a sheep and kept at 37·5°C and 60 per cent. R.H. which are the optimum conditions for oviposition (Murray 1957*b*). After 48 hr 106 eggs had been attached to the fine hairs and two to the coarse hairs. Of the latter, one was attached to a tapering tip and the other to the base of a hair.

Two other collections of lice were exposed to the same conditions of temperature and humidity and hairs from the axilla were placed with one and hairs from the inguinal region with the other. On the hairs from the axilla region, 194 lice attached 21 eggs to the fine fibres, 21 to the thin ends of the coarse fibres, and four to the bases of the coarse fibres. On the hairs from the inguinal region, 191 lice attached 26 eggs to the fine fibres and 41 to the thin ends of the coarse fibres.

In two further experiments under the same conditions, fine fibres and the basal portions of coarse fibres, from which the tapered tips had been removed, were used. After 48 hr 630 lice had attached 45 eggs to the fine fibres whereas no eggs were attached by another 510 lice to the bases of the coarse fibres.

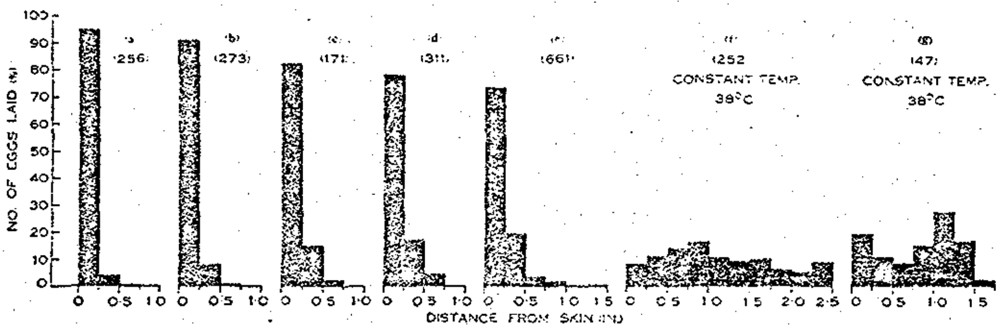

Fig. 1.—Vertical distribution of the eggs of *D. ovis* in the fleece of the sheep. Number of eggs examined in each fleece is shown in parenthesis on each figure. Fleece lengths are as follows: (*a*) 1¼ in.; (*b*) 1¾ in.; (*c*) 2½ in.; (*d*) 3 in.; (*e*) 4 in.; (*f*) 2½ in., temperature 38°C; (*g*) 1¾ in., temperature 38°C.

It can be concluded from these several experiments that the diameter of the base of some of the hair fibres from the legs, face, axilla, and inguinal regions of the sheep was too great to permit *D. ovis* to attach its eggs.

IV. The Influence of Variations in the Temperature of the Environment

(*a*) *The Distribution of the Eggs of* D. ovis *when a Constant Temperature was Maintained within the Fleece of a Sheep*

The temperature gradient in a sheep's fleece was eliminated by circulating water at a controlled temperature through a copper tank which was in contact with the tips of the fleece (see Fig. 2). A skin pedicle *A* which had been made on the side of the thorax of a sheep several months earlier was shaved except for the experimental area *B*. The experimental area was about 1½ by 3 in. in size. Around the pedicle was assembled a wooden framework *C* to support a copper tank *D* at the tip of the fleece of the experimental area. These two structures formed a cylinder around the pedicle and each end was sealed with foam rubber *E*. Thermocouples *F* were placed at different levels in the fleece of the experimental area. The whole apparatus was covered and secured by straps around the sheep. The temperature at the tip of the fleece was kept at 38±1°C so the temperature gradient within the fleece was eliminated.

of ears, and around the nostrils were much lower; at the extremities of the limbs and tail the skin temperature approximated that of the atmosphere. When these sheep were placed in an atmospheric temperature of 30°C, however, the skin temperatures of these regions approximated that of the body.

(ii) *Skin Topography.*—Sheep of certain breeds, such as the Merino, possess numerous skin folds. When adjacent folds were in very close promixity it was found, by means of individual fine thermocouples, that constant temperature zones existed between them and thus increased the area of the 35–38°C temperature zone which favours oviposition.

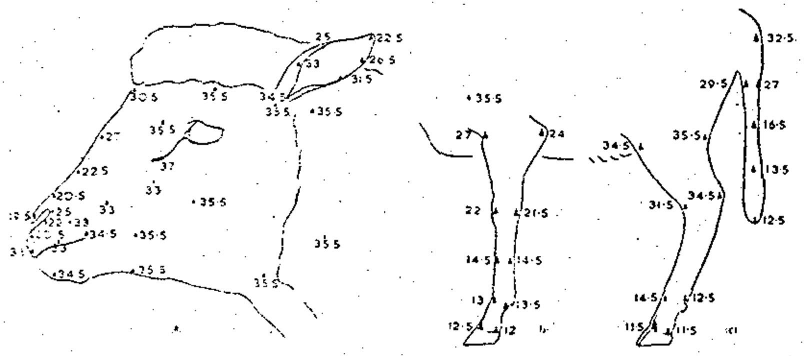

Fig. 3.—Skin temperatures (in °C) on various parts of a sheep when exposed to an atmospheric temperature of 10°C. (*a*) Head; (*b*) fore leg; (*c*) hind leg and tail.

(iii) *Thickness of the Air Blanket within the Fleece.*—Sheep with fleeces which maintained an air blanket from the skin to atmosphere of ½, 1¾, 2¼, and 4 in. thick were housed in a climate room and exposed to constant temperatures of 17±0·5°C, 20±0·5°C, and 25±0·5°C for 18 hr before the temperature gradients within the fleece were recorded with either the thermistor bridge or thermocouple apparatus (Murray 1957*a*). Five areas over the body of each sheep were examined and the mean readings for each sheep when exposed to 20°C are shown in Figure 4. It may be seen that the temperature zone of 35–38°C increased in extent as the thickness of the air blanket increased.

The mean fleece-tip temperature of the 4-in. coat was 17°C in an atmosphere at 17°C, 21°C in an atmosphere at 20°C, and 25·5°C in one at 25°C. That of the ½-in. fleece, however, was 22°C in an atmosphere at 17°C, 22·5°C in an atmosphere at 20°C, and 27·5°C in one at 25°C. Thus, the fleece-tip temperature of the shorter fleece was consistently higher than that of the longer fleece.

In another experiment, in which two sheep were used, the hair covering on the face was found to be ⅛ in. deep and the mean temperature at the tips of the fibres at 11 positions on the face, when they were exposed to 24°C, was 30·2°C for one animal and 31·5°C for the other. Thus the rise in temperature at the tip was even more pronounced when the thickness of the air blanket was only of this depth.

(iv) *Atmospheric Temperature.*—In all the experiments described in Section IV(*b*)(iii) it was found that the fleece-tip temperature was always the lowest in the

Lice were collected daily and placed in the wool in this region. After a week the wool was shaved from the skin and the distribution of the eggs determined. The results are presented in Figures 1(*f*) and 1(*g*) from which it will be seen that eggs were laid throughout the whole length of the fleece.

The vertical distribution of the eggs is therefore determined by the distance to which the temperature zone suitable for oviposition extends from the skin.

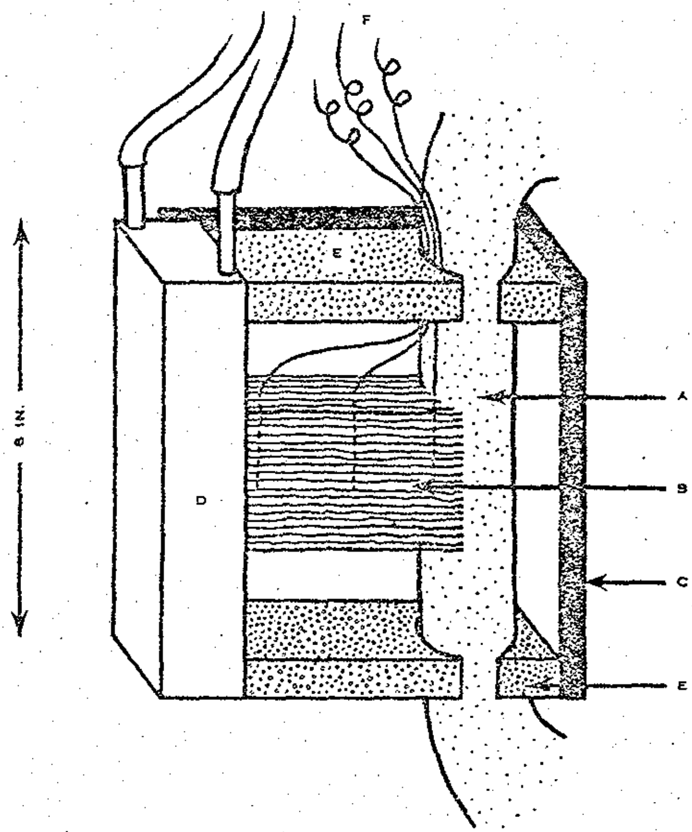

Fig. 2.—Apparatus used to eliminate the temperature gradient in the fleece of a sheep. *A*, skin pedicle; *B*, wool fibres of experimental area; *C*, wooden framework; *D*, copper tank; *E*, foam rubber; *F*, thermocouples.

(b) Factors which Influence the Extent of the Temperature Zone Suitable for Oviposition

(i) *Skin Temperature.*—Two sheep were placed in a cool room in which the temperature was 10°C. After 18 hr the skin temperatures on corresponding parts of the bodies of the sheep were recorded by means of an apparatus embodying a thermistor bridge with a D.C. amplifier. This apparatus was adjusted to record a large temperature range with an accuracy of ±0·5°C. The skin temperatures on the bodies of the sheep were 36·5±1°C, but, as may be seen in Figure 3, the skin temperatures from the elbow joints to the feet, stifles to feet, root to tip of tail, bases to tips gradient and invariably approached that of the atmosphere. Consequently, the area of the 35–38°C zone increased as the atmospheric temperature rose.

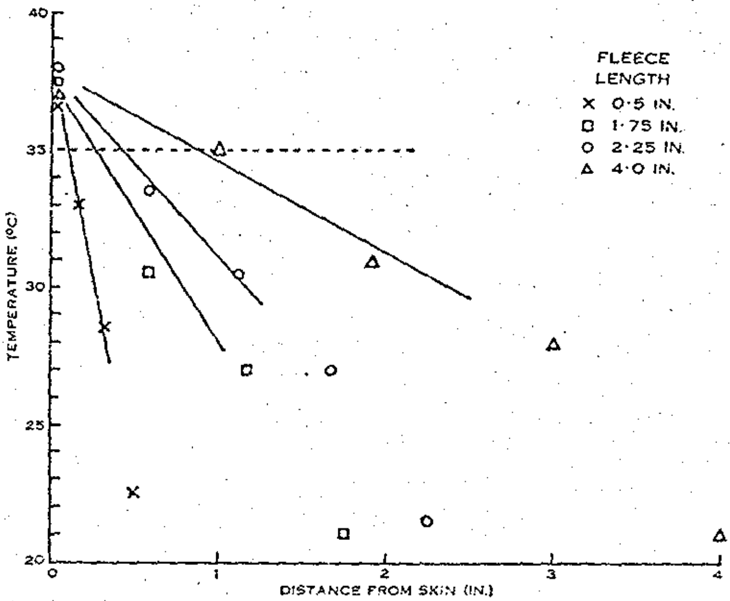

Fig. 4.—Temperature gradients within fleeces of different lengths at an atmospheric temperature of 20°C.

(v) *Solar Radiation*.—Sheep were exposed to solar radiation for 1 hr just before midday when the atmospheric temperature was 43–44°C. The fleece-tip temperatures

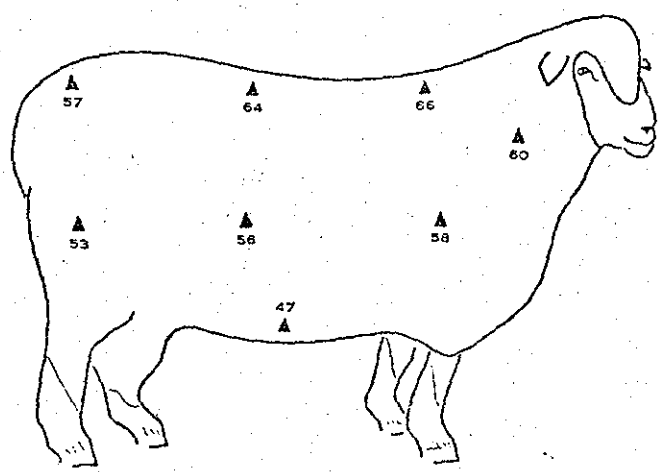

Fig. 5.—Fleece-tip temperatures (in °C) recorded on various parts of the sheep after a 1-hr exposure to solar radiation. The atmospheric temperature was 43–44°C.

recorded from various parts of the body of one of these sheep are presented in Figure 5. These temperatures are representative, and, as may be seen, the highest temperatures were recorded on the back and progressively lower ones down the sides to the belly, which was sheltered from direct solar radiation. The highest temperature recorded on the back of any of the sheep was 71·5°C.

In Figure 6 are shown the temperature gradients which were recorded in the fleece on the back of the sheep referred to in Figure 5. One was obtained immediately after the 1-hr exposure to the sun, just before the sun was obscured by a cloud for 15 min; another was obtained after the sun had been obscured for 5 min; and the third gradient was recorded about 3 hr later during which period the sheep had been continuously exposed to the sun. It will be seen how rapidly the normal gradient can be re-established when the sun is obscured.

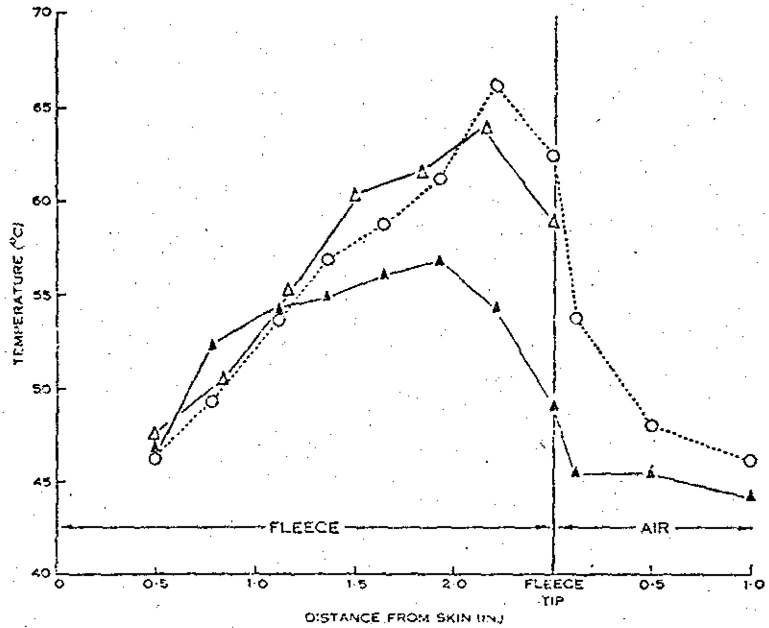

Fig. 6.—Temperature gradients recorded in the fleece of a sheep after exposure to solar radiation. The atmospheric temperature was 44°C (111°F). △ Immediately after an exposure of 1 hr just before midday. ▲ After exposure for 1 hr the sun was obscured by a cloud. This gradient was recorded 5 min later while the sun was still obscured. ○ Immediately after a further continuous exposure of 3 hr.

V. Discussion

Most of the eggs of *D. ovis* were found within ¼ in. of the skin but the thicker the fleece the greater was the zone in which eggs were found. It may be seen in Figure 4, that as fleece thickness increased so did the temperature zone of 35–38°C, which is suitable for oviposition (Murray 1957*b*). A rise in the atmospheric temperature had the same effect and when the temperature of the fleece tip was raised and maintained so that the temperature zone suitable for oviposition extended from skin to fleece tip, eggs were laid throughout the area. This distribution was similar to that obtained when lice were exposed to a constant temperature in a cell with suitable fibres (Murray 1957*b*).

The typical vertical distribution, therefore, is usually the result of an attraction to warmth in stage 1 of the behaviour pattern at the time of oviposition. This leads the louse to the skin where a temperature zone suitable for the completion of stages 2 and 3 is located. When the temperature gradient within the fleece is reversed, as can occur when sheep are exposed to the sun, suitable temperatures are again only to be found near the skin and the lice are driven into this zone by the high temperatures in the outer fleece.

Thus, the distance which the eggs of *D. ovis* may be found from the skin is determined by the extent of the temperature zone suitable for oviposition. Variations in the topography of the skin can increase this area. Merino sheep possess skin folds, which if prominent and in close proximity to one another create a constant temperature zone between them. Principally, however, it is determined by the temperature gradient which in turn is influenced mainly by the depth of the air blanket held between the fibres of the fleece and the temperature at the tip of the fleece. On many sheep the depth of the air blanket and the length of the fleece are the same but when the wool or hair fibres tend to lie parallel to the skin surface, as on the face and feet, the depth of the air blanket is the vertical distance from skin to atmosphere. The factors which influence the temperature of the tip are radiation from the skin, the thermal conductivity of the fibres, atmospheric temperature, and solar radiation. When the air blanket is greater than ½ in. in depth, the two latter, in particular the atmospheric temperature, are more important. However, when the blanket is less than ½ in., radiation from the skin and the thermal conductivity of the coat cause the temperature at the tip to become considerably greater than that of the atmosphere. A consequence of this is that even on the face and legs where the air blanket is thinnest, the depth of the suitable temperature zone next to the skin is adequate to accommodate a louse for oviposition. Thus, provided suitable fibres are present, and provided skin temperature approximates body temperature, *D. ovis* could oviposit anywhere on the body of sheep.

If no fibres are present, no eggs will be found, nor will eggs be laid if the part of the fibre which is in the suitable temperature zone is too great in diameter (Murray 1957*b*). No eggs are found on the bare areas of the sheep because fibres are absent. There are, however, few bare areas on the sheep. The bases of certain hair fibres which are plentiful on the legs, face, axilla, and inguinal region of sheep were shown to be too great in diameter, but mingled with these are many fibres which are of a suitable diameter for oviposition. Consequently, fibre diameter plays little part in determining the lateral distribution of this species on sheep. However, when sheep were exposed to an atmospheric temperature of 10°C, the skin temperature in certain situations on the extremities approached that of the atmosphere and the suitable temperature zone of oviposition next to the skin was eliminated. Skin temperature, therefore, determines the lateral distribution of the eggs.

The mechanisms which regulate the skin temperature of the extremities have been studied on the ears of rabbits (Grant 1930) and cattle (Beakley and Findlay 1955), and the presence of arterio-venous anastomoses has been demonstrated (Grant 1930; Findlay and Goodall 1953). The temperature to which an animal is exposed determines whether these anastomoses dilate or contract and thus decrease or increase the amount of blood circulating in the area distal to the anastomoses. Thus, the skin temperature of the extremities can vary according to the habitat of the animal, during the course of a day, and from one season to another.

There is little information on seasonal variation in the distribution of the eggs of *D. ovis* on the sheep but such variations are well known to occur with *Haematopinus eurysternus* (Nitz.) on cattle. During the summer months, breeding colonies of *H. eurysternus* become established on the ears of cattle (Craufurd-Benson 1941; Matthysse 1946; Brinck 1948). Beakley and Findlay (1955) have shown that, as the atmospheric temperature rises from 15 to 20°C, the skin temperature of the ears of cattle rises from *c*. 17 to *c*. 36°C and remains constant if the atmospheric temperature continues to be above 20°C. Atmospheric temperatures of this order are common during the summer months. Consequently, as the oviposition behaviour of *H. eurysternus* is basically similar to *D. ovis* (Murray 1957*a*), it is highly probable that oviposition by *H. eurysternus* on the ears can only occur when the temperatures are suitable. The establishment of breeding colonies of this louse on the tail and feet of cattle could be governed in a similar manner for it has been shown that at low atmospheric temperatures the skin temperature of these parts can drop to nearly that of the atmosphere (Thompson *et al*. 1954).

Low skin temperatures on the extremities have been reported from mammals as varied as man (Burton and Edholm 1955), reindeer, porcupine, ground squirrel, Stellar's sea lion, dog (Irving and Krog 1955), and the marsupials *Setonyx brachyurus* Quoy & Gaimard (Bartholomew 1956) and *Perameles nasuta* Geoffroy (Murray, unpublished data). It seems likely, therefore, that the skin temperature of the extremities of most mammals falls, in appropriate conditions, and thus governs the distribution of the eggs of many species of lice.

VI. Acknowledgments

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VII. References

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