

ECOLOGY OF LICE ON SHEEP

VII.* POPULATION DYNAMICS OF *DAMALINIA OVIS* (SCHRANK)

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Summary

The numbers of *D. ovis* decline in the spring, remain low during the summer, and increase during the winter. A density of two lice per square inch is necessary in the autumn if numbers are to increase during the winter to 200 per square inch, the density found on heavily infested sheep in the early spring. The time needed for this increase has been calculated using the deterministic matrix model of population increase described by Leslie (1945), and 4-5 months are required when there is only a small mortality.

Thus, when the favourable winter period lasts only 3 months, the increase in louse numbers may be insufficient to sustain the losses which occur in late spring, summer, and early autumn. The factors responsible for these losses determine the density of the louse population at the commencement of winter. Should the winter period last c. 6 months there is usually a direct relationship between the number of lice on a sheep in the late autumn and in the following spring. However, should winter last 9 months it is suggested that other factors become increasingly significant, and determine the eventual size of the louse population.

I. INTRODUCTION

Damalinia ovis (Schrank), the biting louse of sheep, is found on the body and they increase and decline in abundance annually. In much of Australia, there is a decline in abundance in the spring and the numbers of lice remain low during the summer but increase in the late autumn and during the winter (Scott 1952).

It has been shown that on Merino sheep in Australia a density of two lice per square inch is necessary in the autumn if an increase is to occur during the winter. Consequently, any factor which reduces the density below this level during the summer and autumn can determine the number of lice on the sheep in the following spring (Murray 1963). Furthermore it has been observed repeatedly that at times nymphs comprise a major part of the population, whereas on other occasions adults dominate. The age structure of the population is variable, and influences the choice of mathematical model suitable for the study of the rate of increase of louse populations.

The time required for the completion of the life cycle of *D. ovis*, the oviposition rate of females, and the sex ratio of lice in a population are known. Consequently, it has been possible to calculate§ the time required for populations to increase from two lice per square inch to those observed by the end of winter on heavily infested sheep, both under extremely favourable conditions of no mortality, other than old age, and in the presence of a slight to moderate mortality. It has been found that *D. ovis* has a

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§ Calculations were made using the CSIRO CDC 3200 computer in Sydney.

relatively low reproductive potential compared with other species of lice (Murray 1965), and the significance of this finding in the population dynamics of this species is discussed.

II. THEORETICAL STUDY OF POPULATION DYNAMICS

(a) *Mathematical Model*

In the present problem we wish to describe the development of a small population with an unstable age distribution. The deterministic matrix model as described by Leslie (1945) and Moran (1962) was adopted. In this model the female population is considered at discrete intervals of time, $t = 0, 1, 2, \dots$, in terms of some unit of time. The population is divided into age groups, using the same unit of age as is adopted for time. Thus suppose that $n_{x,t}$ is the number of females alive in the age group $(x, x+1)$ at time t . Let P_x be the fraction of females in age group $(x, x+1)$ at the beginning of a time interval, which are still alive in age group $(x+1, x+2)$ at the end of the time interval. Let the number of daughters born during a time interval, to each female in age group $(x, x+1)$ at the start of the time interval, and still alive in age group $(0, 1)$ at the end of the time interval, be F_x . We suppose that we need consider m age groups, so that all the individuals belonging to age group $(m, m+1)$ at a given time die during the next unit time interval. Then the age structure of the female population at time t may be given by a vector

$$\mathbf{n}_t = \begin{bmatrix} n_{0,t} \\ \cdot \\ \cdot \\ n_{m,t} \end{bmatrix}$$

The population vector at the time $t+1$ is obtained by adding to the first age group all the individuals born in $(t, t+1)$ and carrying on the proportion of each age group which survives the interval to the next age group. Thus

$$\begin{bmatrix} n_{0,t+1} \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ n_{m,t+1} \end{bmatrix} = \begin{bmatrix} F_0 & F_1 & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & F_m \\ P_0 & & & & & & & & \\ & P_1 & & & & & & & \\ & & \cdot & & & & & & \\ & & & \cdot & & & & & \\ & & & & \cdot & & & & \\ & & & & & \cdot & & & \\ & & & & & & \cdot & & \\ & & & & & & & P_{m-1} & 0 \end{bmatrix} \begin{bmatrix} n_{0,t} \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ n_{m,t} \end{bmatrix}$$

where all elements except those indicated in the above $(m+1) \times (m+1)$ matrix \mathbf{M} are zero, i.e. $\mathbf{n}_{t+1} = \mathbf{M}\mathbf{n}_t$, so $\mathbf{n}_t = \mathbf{M}^t\mathbf{n}_0$, where \mathbf{n}_0 is the initial population vector.

An improvement to the model would be to suppose that each individual in age group $(x, x+1)$ has a probability P_x of surviving to the next age group instead of assuming, as we have done, that the fraction of the population in age group $(x, x+1)$ surviving to the next age group is P_x . Then the number of individuals surviving to the next age group is a random variable, and not a fixed proportion of the number in

the age group. However, it is true that a population vector given by the deterministic model is the expected value of the corresponding vector of this probabilistic model, and is best understood in this sense (Pollard 1966; Sykes 1966).

It should be noted that it is necessary to have the size of the unit of age and time not too large compared with the life span of the species, otherwise the "lumping" of the mortalities and fertilities can cause error. All calculations are in terms of the female population, so to calculate the total population the sex ratio must be known.

The distinction between the actual population and the conceptual population should always be borne in mind but, in spite of the restrictions mentioned, the model we have used is a useful tool for finding the likely effects of selected mortalities on population growth. The restrictions were thought to be unimportant as the main conclusions of the paper are only semiquantitative. We are interested in the likely effects of a few broad types of age dependent mortalities.

(b) *Details of Model*

The mathematical assumptions are as follows:

- (1) The initial density is one female and one male, the female louse is fertilized and ready to commence oviposition.
- (2) All females lay fertile eggs throughout their lives, and the sex ratio remains one female to one male.
- (3) In all calculations a time unit of 5 days is used. The life cycle requires 35 days (7×5 days) comprising 10 days (2×5) for egg development, 20 days (4×5) for nymphal development, and 5 days preoviposition period for females.
- (4) In every 5-day unit, 1.6 female eggs are laid, and egg-laying females live 15, 30, or 60 days (i.e. $\times 3$, $\times 6$, or $\times 12$ 5-day units). Population vector sizes are $m = 10, 13, 19$, and in each matrix \mathbf{M} , $F_i = 1.6, i = 8, \dots, m$.
- (5) Initially the population growth under extremely favourable conditions was studied when there was no mortality other than old age. In these examples $P_i = 1, i = 1, \dots, m$, and $m = 10, 13$, or 19 .
- (6) The effects of the following mortalities were studied: where $m = 10, 13$, or 19 and
 - (i) $P_0 = 0.90, P_1 = 0.90, P_2 = 0.80, P_3 = 0.85, P_4 = 0.90, P_5 = 0.90$, and subsequent $P_i = 1$ (c. 19% mortality of eggs and c. 45% mortality of nymphs);
 - (ii) $P_0 = 0.80, P_1 = 0.875, P_2 = 0.80, P_3 = 0.85, P_4 = 0.85, P_5 = 0.85$, and subsequent $P_i = 1$ (c. 30% mortality of eggs and c. 51% mortality of nymphs).
- (7) Population vectors were calculated in each case at successive time intervals with the parameters F_i and P_i kept constant until the total nymphal and adult populations reached 200.

(c) *Biological Validity of Mathematical Assumptions*

- (1) *Number of Animals at Time Zero.*—A density of two lice per square inch is required on Merino sheep in the autumn if the population is to increase markedly

during the winter. As *D. ovis* are fairly evenly dispersed over the body of a sheep, this represents the density of a total population of *c.* 4000 lice (Murray 1963).

(2) *Sex Ratio*.—The sex ratio of *D. ovis* is usually 1 : 1 (Scott 1952).

(3) *Mean Duration of a Generation*.—During the winter months, when solar radiation is not intense, the temperatures within the fleece are 36–37°C near to the skin, falling in a steady gradient to atmospheric temperature at the tip of the fleece, and fluctuations of the temperature near the skin are small. The temperature, and probably the humidity, of the habitat in which eggs develop and hatch when populations are increasing in numbers is therefore fairly constant. Consequently, the data obtained by Scott (1952) when *D. ovis* was exposed to a constant temperature may be accepted, particularly as they correlate well with her determination of the length of the life cycle on sheep.

The eggs of *D. ovis* require 10 days to develop and hatch, the three nymphal instars require 7, 5, and 9 days respectively to complete development, and the preoviposition period of the female is 3–4 days. The minimum length of the life cycle from egg to egg is *c.* 34 days (Scott 1952). To facilitate calculations it was taken as 35 days, comprising 10 days for egg development, 20 days for nymphal development, and 5 days preoviposition period for the female.

(4) *Frequency of Egg Laying and Longevity of Females*.—Eggs develop singly in female *D. ovis*, and not until one egg has been laid does another develop. At least 24 hr are required for development. Scott (1952) found the rate of oviposition of laboratory-reared *D. ovis* to be one egg every 2–3 days, i.e. *c.* two eggs every 5 days or *c.* one female egg every 5 days. This value is probably low so it was taken that 1·6 female eggs are laid every 5 days.

Scott (1952) was able to keep some adult *D. ovis* alive for 20 days on a diet of skin scurf and yeast. It seems likely that on a sheep they live longer, and consequently calculations were made assuming fertilized females lived 15, 30, or 60 days.

(5) *Extremely Favourable Conditions*.—There is no mortality other than due to old age. It was further assumed that the oviposition rate of *D. ovis* is constant throughout the life of the female, and that all of the eggs laid are fertile.

(6) *Mortalities*.—Dead eggs, nymphs, and adults are seen frequently in the fleece of sheep.

Eggs were removed from two sheep kept indoors by shaving the wool from the skin every 2–3 weeks for 6 months. Newly laid eggs were identified (Murray 1960), and exposed to 37°C at 54% R.H. The number which had hatched, and the stage of development reached by those which failed to hatch was determined. In all, *c.* 3000 eggs were removed, and the percentage of eggs which hatched was usually 60–80% with a range of 30–90%. Furthermore, *c.* 18%, range 5–45%, of the eggs collapsed, and the absence of macroscopic evidence of morphogenesis suggested they were infertile. Thus there was frequently a 20–40% mortality of eggs, many of which were apparently infertile.

The nymphal mortalities selected were considered to be representative of the slight to moderate losses a population could incur, and correspond to losses in the vicinity of 20% of each of the three nymphal stages.

(7) *Time Required for Population Increase*.—The time required for the density of lice per square inch of skin to increase from 2 to 200 nymphal and adult lice was

determined. This is equivalent to an increase in the total number of lice from *c.* 4000 on a sheep in the autumn to 0.4–1 million in the spring, the number found on heavily infested sheep (Murray 1963).

III. RESULTS

The length of time required for a population of *D. ovis* to increase from 2 to 200 lice (nymphs and adults), assuming that there is no mortality other than due to old age, is shown in Figure 1(a). Should egg-laying females live 60–30 days under these

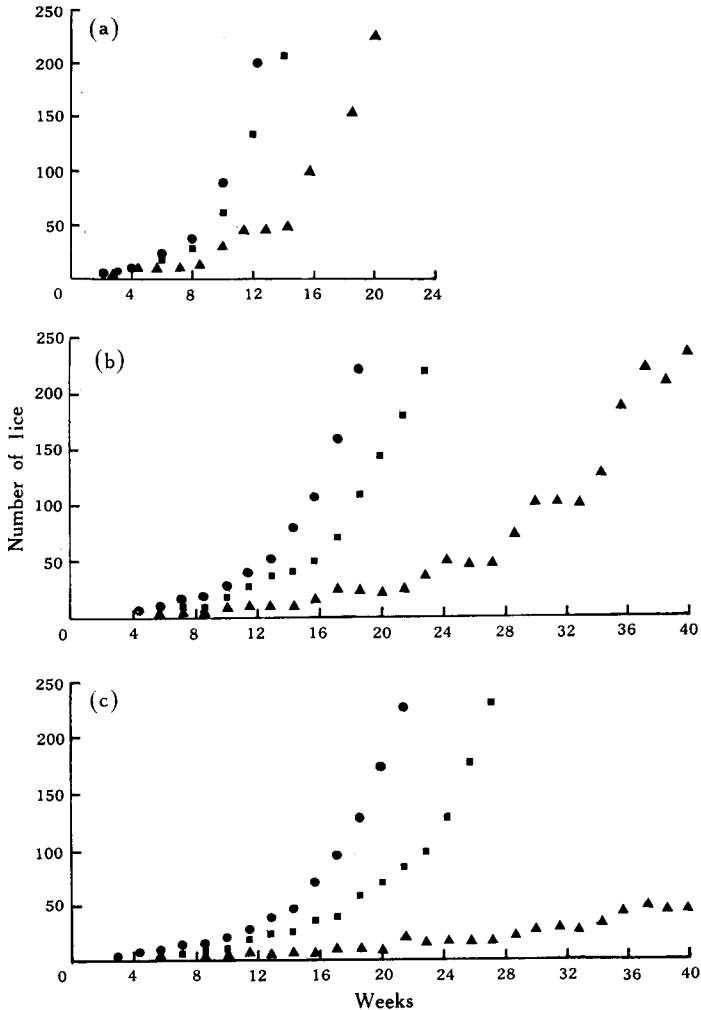


Fig. 1.—Calculated increase in numbers of nymphs and adults from one fertilized female of *D. ovis* for zero mortality per 5-day unit (a), for a mortality of *c.* 19% eggs and *c.* 45% nymphs (b), and for a mortality of *c.* 30% eggs and *c.* 51% nymphs (c). Adult fertilized females live 60 days (●), 30 days (■), or 15 days (▲).

optimal conditions 3–3½ months are required, and 4–5 months if females only live 15 days. When there is a slight mortality of only 20% of eggs and 45% nymphs per 5 days,

4½–5½ months are required for the population to increase to 200 if females live 60–30 days, and 9–10 months if they live only 15 days [Fig. 1(b)]. If the mortality is 30% of eggs and 51% of nymphs, 5–6½ months are required if egg-laying females live 60–30 days, and if they only live 15 days the population is still less than 50 after 10 months [Fig. 1(c)]. A sudden mortality of 80% can delay increase of these populations 5–8 weeks, 6–10 weeks, and 8–15 weeks if females live 60–30 days, as may be deduced from Figures 1(a), 1(b), and 1(c) respectively.

The length of life of fertilized females in the population is critical because only *c.* two female eggs are laid every 5 days. Should they live at least 4 weeks moderate losses of eggs and nymphs can be tolerated, the population continues to increase, and the age structure rapidly becomes stabilized. However, should they live less than 4 weeks a severe retardation in population increase can result, and the age structure of the population becomes unstable even when there is no mortality of eggs and nymphs (Figs. 1 and 2).

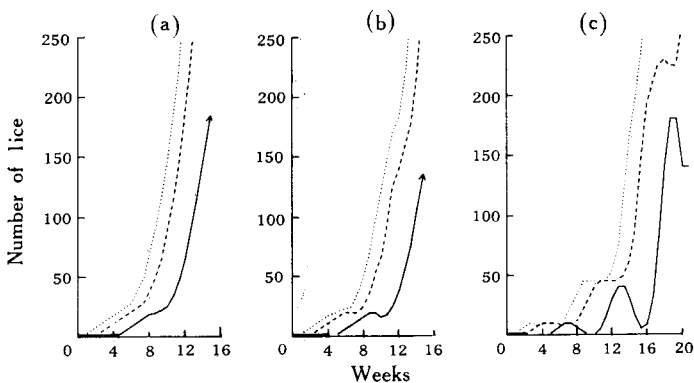


Fig. 2.—Calculated age structure of populations of *D. ovis* where the initial population is one fertilized female, and there is no mortality other than old age. Adult fertilized females live 60 days (a), 30 days (b), and 15 days (c). ····· Eggs. ---- Nymphs. ——— Adults.

The innate capacity for increase, r (Andrewartha and Birch 1954, p. 43), of *D. ovis* is low, about 0·433, 0·456, and 0·459 per week where the females live *c.* 30, 60, and 90 days respectively, and there is no mortality other than due to old age. The equivalent values for the finite increases per female per week are 1·54, 1·58, and 1·58. These were calculated iteratively by the “rule of false position” to solve r in equations

$$\int_0^{\infty} e^{-rx} l_x m_x dx = 1,$$

where l_x is the fraction of the initial population surviving until age x , and m_x is the rate at which eggs are laid by a female of age x (Andrewartha and Birch 1954). Using these values of r it is seen that a daily mortality of only 6·5% of all components of the population is sufficient to prevent an increase in numbers. Consequently, relatively small mortalities occurring regularly may drastically reduce numbers, and the effects of a sudden calamity can be prolonged.

IV. DISCUSSION

The number of lice declines in the late spring, remains low during the summer, and increases in the winter. The six "winter" months (i.e. late autumn, winter, and early spring) comprise a period when the full reproductive potential of *D. ovis* in its particular environment on a sheep may be realized whereas the six summer months do not.

Three known causes of mortality during the summer in Australia are shearing, solar radiation, and thunderstorms (Murray 1963, 1968). Shearing removes all of the fleece habitat except $\frac{1}{4}$ – $\frac{3}{8}$ in. near the skin, and thus can remove 30–50% of the population. A major effect, however, is the alteration of the habitat so that the microclimate becomes more variable. Solar radiation creates in the fleece lethal temperatures which kill both adults and nymphs, and, if prolonged, can reduce the number of eggs laid and even kill eggs. The mortality from a single exposure to the sun may not be great but it can occur daily for 4–5 months. Mortalities of 5% have been demonstrated experimentally when lethal conditions, similar to those created by solar radiation, are produced in a fleece (Murray 1968). As a daily mortality of *c.* 6.5% is sufficient to prevent population increase, the accumulative effect of these mortalities is likely to be severe in most instances, particularly should they reduce the length of life of female lice to less than 4 weeks. Fleeces may be saturated with rain, and if they remain sodden for 6 hr nymphal and adult lice are drowned. Furthermore, eggs fail to hatch when the R.H. near the skin remains over 90%. Mortalities as high as 90% of nymphs and adults can occur suddenly when the fleece of a sheep has been soaked in a thunderstorm (Murray 1963).

The long-term effect of such factors is influenced by the initial density of the population. Should the density be low the chances that it may be reduced below two lice per square inch are greater, and even though the population may be maintained, it is unlikely that the number of lice will increase noticeably during the six winter months. The speed of recovery depends on the degree of realization of the louse's reproductive potential, which varies between sheep as heavy louse infestations do not develop on all sheep even when kept under favourable climatic conditions. However, because *D. ovis* has a low reproductive potential, the differences between the environments on individual sheep need not be great to produce differences in the size of louse populations. The ultimate size of the population is influenced greatly by the length of time favourable conditions prevail but 4–5 months are required even when there is only a relatively small constant mortality. Because the favourable period for multiplication in much of Australia is *c.* 6 months there is usually a direct relationship between the size of a louse population in the early spring and the previous autumn, i.e. those sheep which have most lice at the beginning of the winter have most lice at the end. The number of lice on a sheep in the autumn can be determined largely by the severity of factors such as shearing, solar radiation, and thunderstorms, which operate during the summer. However, the effects of solar radiation and thunderstorms are influenced by the behaviour of the individual sheep, which may shelter under a tree during a thunderstorm or from the sun. As the consequence of such behaviour is not manifest for several months, it can be difficult to determine the factors which have influenced the abundance of lice on individual sheep.

Under extremely favourable conditions of no mortality [Fig. 1(a)], populations do not increase rapidly in numbers until about the tenth week when the contributions of the third generation are made. Therefore, where the favourable winter period is shortened to *c.* 3 months, the increase in louse numbers may be inadequate for the population to survive the losses which occur during the summer. This may well account for the rareness of sheep with lice in western Queensland. However, the numbers of lice on unshorn sheep sheltered from the weather do not increase indefinitely, and it appears that, under these conditions, factors other than those discussed determine the eventual size of the louse population. It is likely that such factors may be more important in determining the ultimate numbers of *D. ovis* in the cooler zones of the world, where the duration of the adverse summer period may be only 3 months and the favourable winter period may extend to 9 months.

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