SIMULATION OF PASTURE LARVAL POPULATIONS OF
HAEMONCHUS CONTORTUS

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Summary
Assumptions regarding egg hatching and larval development and survival, together with actual climatic data were used to construct a model to simulate larval populations of Haemonchus contortus on pasture. Over a two-year period predicted patterns of larval concentration on the pasture showed substantial agreement with measured values.

I. INTRODUCTION
Studies at Armidale on the ecology of helminthoses have provided information on the populations of both parasitic and free-living stages of sheep nematodes under varying seasonal conditions. The complexity of the climatic, nutritional, physiological and immunological factors which interact in the epidemiology of parasitic disease is such that even given this information, it is difficult to predict the occurrence or likely consequences of worm infections in grazing sheep. The technique of computer simulation appeared to offer an attractive method for combining this diverse collection of data in such a way that it not only summarized our present knowledge of the system but also possessed some predictive value.

This first attempt at the analysis of the system has been restricted to the free-living stages of the abomasal parasite Haemonchus contortus. This parasite is of major economic importance in the New England environment, and there is probably more information available on its climatic requirements than for any other nematode infecting sheep. Raclifffe et al (1969) have constructed a model of the parasitic stages of the life cycle which they used to simulate host-parasite interactions in real sheep. The significance of their work was not only that the simulations were successful, but also that they drew attention to some hitherto unsuspected physiological differences between sheep which may be of great importance in the response to H. contortus infection.

The aims of the present study were to simulate the fluctuations in the population of infective H. contortus larvae on the pasture, and to compare the simulated results with actual results obtained from a Phalaris-white clover pasture grazed by infected sheep over a two-year period.
II. INPUTS AND ASSUMPTIONS

The major inputs for the model are meteorological data from July 1969 to May 1971. Daily observations of maximum and minimum screened air temperature, relative humidity at 1400 h, precipitation, and evaporation from an Australian standard evaporimeter were obtained from the records of the C.S.I.R.O. Pastoral Research Laboratory, Armidale. The availability of both green and dry herbage was measured at approximately six-weekly intervals over the same two-year period on Phalaris-white clover pastures grazed at a similar stocking rate to the experimental pasture. Daily egg deposition rates were based on mean monthly egg counts of the flock of infected sheep studied by Roe, Southcott and Turner (1959). These counts were multiplied by the stocking rate and the estimated daily faecal output per sheep to give the number of eggs deposited per acre per day. The initial number of larvae on the pasture was set at zero.

The assumptions regarding the development and survival of *H. contortus* from the egg to the third-stage infective larvae (L3) were as follows:

(i) An Haemonchus egg has a maximum life of 5 days. Eggs not hatching on the day of deposition are available for hatching for up to four days (Donald, 1968-69).

(ii) For hatching, the minimum daily temperature must exceed 10°C (Swan 1970) and the maximum must be equal to or greater than 18°C (Dinaburg 1944). The percentage of eggs which hatch was assumed to vary between 50 per cent at 18°C and 100 per cent at 21°C.

(iii) Once hatching has occurred, the third-stage must be reached within 21 days or death occurs. Conditions necessary for development of hatched eggs to L3 are estimated by summing precipitation (P) and evaporation (E) on a daily basis for up to three weeks from hatching. If $\sum P / \sum E$ exceeds 1 after one week, 90 per cent develop to L3. If it takes 2 weeks to exceed 1, 70 per cent go to L3, and 50 per cent if $\sum P / \sum E$ takes 3 weeks to exceed 1. In addition, the mean maximum temperature must be equal to or greater than 18°C over the whole developmental period.

(iv) The proportion of L3 larvae which migrate on to the pasture is a function of the proportion of green material in the available herbage. Silangwa and Todd (1964) showed that the proportion of the L3 population on the pasture increased with increasing humidity. In the absence of data on humidity within the pasture we assumed that this would be a function of the proportion of green material in the herbage. Once larvae are on the pasture, they remain there as no appreciable downward movement occurs (Silangwa and Todd 1964).

(v) The death rate of the entire L3 population has been assumed to be a function of daily maximum temperature and relative humidity. The proportion of the larvae which die each day is given by the expression:—

$$LD = \sqrt{e^{-R/15} / I + 200 e^{-T/10}}$$

(F. H. W. Morley, unpublished)

where $LD =$ larval death rate

$T =$ maximum temperature in °C

$R =$ relative humidity
e — exponential.

Although predation of eggs and larvae by other nematodes and fungi is known to occur, no quantitative information on predators is available. The assumed mortalities of eggs and larvae described above therefore include an unknown proportion attributable to predators. A simplified flow diagram for the model is shown in Figure 1.

III. THE COMPUTER MODEL

The above assumptions have been incorporated into a simulation programme which causes the computer to trace out, day by day, the changes occurring in the number of eggs waiting to hatch, eggs hatching, larvae undergoing development and so on, through to the numbers migrating up the grass.

To advance the simulation from each day to the next, first the input data pertaining to the next day is obtained. Climatic inputs are read from a table, while egg deposition rates and pasture values are obtained by linear interpolation between the tabulated values.

Those variables that collectively define the current internal state are then updated. These include the number of eggs in each age class from one up to five days old, number of developing larvae in each age class up to three weeks old, and current population of stage 3 larvae. The rainfall, evaporation and temperature on previous days for the past three weeks must also be retained.

In general the updating of these variables is achieved by allowing the transactions for the present day (n) to provide the values for the next (n+1) day. In the case of eggs, however, the number hatching is subtracted before transferring the number in one age class to the next. The proportion hatching each day is calculated from temperatures in accordance with assumption (ii). Similarly, for the larvae, subtractions from the number to be passed on
to the next age group are made whenever the retained climatic values satisfy the criteria of assumption (iii).

The L3 population is incremented by the numbers calculated from assumption (iii) and decremented each day by the proportion dying, as calculated from temperature and humidity according to assumption (v). Finally, the concentration on the grass is calculated from amounts of green and dry pasture using assumption (iv).

It was considered desirable to have the output in graphical form. Since high precision was not needed it was possible to accommodate, in a very compact layout, graphs against time of all of the more important variables. With this type of output one can readily monitor all phases of development and ensure that the intended assumptions are being satisfied.

IV. RESULTS

From the daily computation of the number of infective larvae per acre, together with the appropriate figures for the proportion migrating on to the pasture and the pasture availability, the number of larvae per unit weight of herbage was calculated. The predicted concentrations of larvae on the pasture for the period from July 1969 to May 1971 are shown in Figure 2. Also shown are the observed concentrations of *H. contortus* larvae as measured by the method of Heath and Major (1968) on the experimental pasture over the same period.

![Graph showing predicted and observed concentrations of *H. contortus* larvae](image)

**Fig. 2.** — The predicted (——) and observed (●) concentrations of *H. contortus* larvae on the pasture from July 1969 to May 1971.

V. DISCUSSION

The good agreement ($r^2 = 0.86$) between predicted and observed results encourages the view that the fundamental structure of the model is sound. However, the arbitrary nature of some of the assumptions relating temperature and moisture conditions to larval development means that further validation of the model in other environments will probably be required before its predictions can be regarded with confidence.
With these reservations, it seems appropriate to use the model in its present state to explore some of the arbitrary assumptions. For instance, by systematic coverage of a range of minimum and maximum critical temperatures and precipitation-evaporation ratios, it should be possible to adjust the predicted first occurrence of larvae in the spring to coincide more precisely with the real situation and thus derive better estimates of these parameters under field conditions. The lack of such information was made apparent during the construction of the model, as laboratory studies reported in the literature were invariably made under constant, controlled conditions.

Although a full sensitivity analysis of the model has not been made, it is apparent already that moisture is a critical factor during those months when temperatures are high enough for larval development. The effects of moisture stress are shown in both the simulated and real results for January 1971 when a sharp decline in larval numbers followed a two-week dry spell in an otherwise wet season. In addition to further refinements to and investigations with the present model, it is intended to integrate it with a model of the epidemiological response of a grazing flock of sheep to the various levels of pasture contamination. Such an integrated model of the life cycle of *H. contortus* should be a useful aid in the study of the effect of management factors on the occurrence of outbreaks of haemonchosis.

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VII. REFERENCES