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THE EPIDEMIOLOGY OF NEMATODE PARASITISM IN SHEEP WITH PARTICULAR REFERENCE TO MANAWATU DISTRICT

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Introduction.

The following account is a summary of experiments that have been conducted on the epidemiology of nematode parasitism in Manawatu district. In different parts of New Zealand there are likely to be differences in the incidence and intensity of parasitism among the various species of parasites.

In order that control measures may be effectively applied, an understanding of the factors which influence the incidence of parasitism need to be understood. Such knowledge will permit the application of preventive measures of control and at the same time will enable the more efficient application of anthelmintic measures .

The present approach to the problem is mainly ecological and has been made on the hypothesis that studies of the bearing of environment on the incidence of parasitism will have especial reference to the problem in New Zealand, for our systems of pastoral farming are unique. Complete understanding of the factors that are involved in determining the epidemic picture of nematode parasitism can come about only through the piecing together of the results of a series of experiments carried out over an extended period. One field of study, a zoological one in the present instance, cannot result in a solution of the nematode problem. Such fields of study as the role of nutrition and others are also fundamental to gaining the desired knowledge necessary to combat parasitism in sheep.

In the present studies considerable attention has been paid to the devising of technical methods of study in order that data may be compiled that will be of comparative value and amenable to checking by different workers. Complete solution of the technical difficulties has not been accomplished.

Species Present in New Zealand.

The writer (1934) has recorded the species of nematodes that he has found in sheep in New Zealand. The range of species is similar to what has been found for this host in other temperate countries.

The following species have been found:—

Stomach .... **Haemonchus contortus**
Ostertagia circumcincta
O. trifurcata
O. ostertagi
Trichostrongylus axei

Small intestine	Strongyloides papillosus
	Trichostrongylus colubriformis
	T. vitrinus
	T. capricola
	Nematodirus filicollis
	Nematodirus spathiger
	Nematodirus abnormalis
	Nematodirus helvetianus
	Cooperia curticei
	Cooperia punctata
	Cooperia oncophora
	Cooperia mcmasteri
	Bunostomum trigonocephalum
	Capillaria longipes
Caecum and colon	Trichuris ovis
	Oesophagostomum venulosum
	O. columbianum
	Chabertia ovina
Lungs	Dictyocaulus filaria
	Muellerius capillaris

NOTEWORTHY ABSENCE OF SPECIES OF SHEEP PARASITES FROM NEW ZEALAND

It is noteworthy that **Trichostrongylus rugatus** has so far not been found in sheep in this country, nor have certain species of **Cooperia** that appear to have recently been acquired by sheep from wild ruminants. **T. rugatus** receives the common name "bankrupt" worm in South Africa, and by inference it is desirable to insure that it does not gain entrance to New Zealand.

RELATIVE ABUNDANCE OF SPECIES IN NEW ZEALAND

Worms of the Stomach.

Haemonchus contortus, Ostertagia circumcincta and **Ostertagia trifurcata** are found abundantly in sheep throughout New Zealand. In Manawatu district it is customary for **Ostertagia** species to be numerous in lambs every year. **Haemonchus**, on the other hand, does not necessarily occur in large numbers in successive years and it is not unusual for there to be a lapse of a few years between periods of high populations in lambs. **Ostertagia ostertagi,** a cattle parasite has been found occasionally in sheep in small numbers in Manawatu district and no doubt this species has similar incidence in sheep in other parts of New Zealand. **Trichostrongylus axei,** while being a common parasite of sheep, does not appear to attain to large populations, and probably the same holds for other parts of the country.

Worms of the Small Intestine.

Trichostrongylus colubriformis and **Trichostrongylus vitrinus** occur in sheep in large numbers throughout the country. Of the small intestinal worms, they are probably the most economically important species. **Trichostrongylus capricola,** a goat species, has occasionally been found in small numbers in sheep. **Cooperia curticei** is a common parasite in sheep of this country and may prove to be of greater importance than has hitherto been recognised. Populations of over 20,000 have been found in lambs in the autumn and at that level may be ranked, in economic importance, with **Trichostrongylus** species. **Nematodirus filicollis** and **Nematodirus spathiger** occur abundantly, it being the exception for them to be absent from lambs in the first nine months of life. **Nematodirus abnormalis** and **Nematodirus helvetianus,** which are essentially cattle parasites, are found in small numbers in lambs. Worms of this genus have not been clearly associated with ill effects on their hosts. **Strongyloides papillosus** has a high incidence in lambs but intensity of parasitism does not attain to the high level found for **Tricho-**

strongylus, Cooperia and **Nematodirus** and accordingly this species has been regarded as of little significance. It is possible, however, because of its ability to infect hosts percutaneously, that it may prove to have some injurious effect on very young lambs. **Bunostomum trigonocephalum** does not occur in the large populations that have been recorded in sheep in warmer climates. Periodically reports are heard of its high incidence in various districts. While populations are always much smaller than for other species found in the small intestine of sheep, it is well to remember that relatively few worms of this species are able to cause injury to a host. In this **Bunostomum** shares the characted of hookworms in general. **Capillaria longipes,** though a not uncommon species, does not occur in populations of more than a few individuals and economically speaking may be disregarded.

Parasites of the Caecum.

Trichuris ovis has a high incidence in lambs though individual populations are usually small, one hundred worms being numerous for the species. While **Trichuris** is not regarded as an important species in sheep the writer believes, when populations in the vicinity of one hundred worms occur, that there is appreciable injury to the caecal wall. **Oesophagostomum venulosum** has similar incidence and in intensity of parasitism to **Trichuris.** It appears to cause little, if any, injury to lambs. **Oesophagostomum columbianum** has not been found by the writer in sheep in Manawatu district, though it has been found by others, sporadically, in other parts of this country. It is certainly not of the same significance in New Zealand as it is in some other countries, notably Australia.

Parasites of the Colon.

Chabertia ovina has an incidence and intensity of parasitism similar to **Trichuris** and **Oesophagostomum venulosum.** This species may prove to be of greater significance than has been previously recognised, particularly when in association with heavy stomach and intestinal parasitism by other species.

Parasites of the Lung.

In Manawatu district the incidence of **Dictyocaulus filaria** is high in lambs during the autumn, however, the writer has experienced difficulty in securing clearcut evidence that mortality, due to this species alone, occurs in this district. Localised pneumonia is a common pathological effect resulting from the presence of this species but, provided that the well being of the hosts from other points of view is taken care of, the lambs appear to be able to throw off parasitism successfully. **Muellerius capillaris** is common, the pin head nodules on the lung surface being a familiar sight to those involved in slaughtering sheep. Sheep appear to suffer little effect from the presence of this parasite.

SEASONAL INCIDENCE AND SUCCESSION OF PARASITES.

Parasitism in lambs in Manawatu district takes the form of a succession of groups of parasites. The succession is more clearly defined in connection with the onset of parasitism and the peaks of parasitism than with its decline in incidence and intensity.

The annual appearance of the lambs in the spring sets the cycle of parasitism in motion. The first wave of parasites consists of the following abundant species:—

Ostertagia circumcincta
Ostertagia trifurcata
Nematodirus filicollis
Nemotodirus spathiger
Strongyloides papillosus
Trichuris ovis
Chabertia ovina.

These tend to accumulate rapidly, according to their population potentialities, from the time lambs begin to nibble grass. Parasitism usually reaches a mid-summer peak following which there is an autumn (May or June) recession in populations. In some seasons, however, in Manawatu district, parasitism by this group at a high level may extend into winter. Whether the latter happens or not, the peak intensity of parasitism occurs before that of the groups about to be discussed.

In the second wave of parasitism **Haemonchus contortus** is the dominating species. Although this species may be acquired by lambs in small numbers in early spring, it is not until January, February and March, in Manawatu district, that its population accumulates most rapidly. The peak of parasitism by this wave succeeds that of the first group of species. The intensity of parasitism diminishes to a low level in late autumn.

Trichostrongylus colubriformis, Trichostrongylus vitrinus, Trichostrongylus axei and Cooperia curicei take part in a third wave of parasitism. While these species may accumulate during early autumn in large numbers in some seasons, usually they do not attain to a peak until late autumn and early winter. Parasitism by these species may continue at a high level into the second year of life of sheep; probably this occurs in years of heavy parasitism. In Manawatu district in the present year large populations **Trichostrongylus,** in the vicinity of thirty thousand worms were present in August. The writer has found greatest populations of **Cooperia curticei** and **Strongyloides papillosus** in the second year of life of sheep. In regard to the latter species reference has already been made to its early presence in the life of lambs; it appears to have a fluctuating incidence and to this extent differs from other species.

THE ROLE OF PREGNANT AND LACTATING EWES IN CONTAMINATING PASTURE WITH EGGS OF NEMATODES

In order to obtain knowledge of the role of breeding ewes as vectors of the parasites of lambs the cycle of nematode parasitism in a flock of aged ewes, as shown by numbers of eggs found in faeces, was observed during pregnancy and lactation. The flock was kept in one paddock throughout the experiment.

It was found that the following species of worms parasitised the ewes:—

Haemonchus contortus
Ostertagia spp. (probably both **O. circumcincta** and **O. trifurcata)**
Strongyloides papillosus
Nematodirus filicollis
Cooperia curticei
Trichuris ovis
Capillaria sp.
Chabertia-Oesophagostomum group.

Examination was not made for the presence of lungworm larvae on faeces.

The eggs of **Ostertagia** and **Trichostrongylus,** being difficult to differentiate, it was not possible to determine their numbers accurately, but as post mortem examinations made in other experiments have shown that **Trichosstrongylus** were present in low numbers in mature sheep, the data obtained in this experiment have been regarded as pertaining to Ostertagia. Eggs of **Haemonchus contortus, Ostertagia, Cooperia curticei** and the group **Oesohagostomum-Chabertia** were the most abundant, though their numbers compared with what obtains among lambs, were low. There was considerable fluctuation among sheep in the intensity of parasitism, most animals having low counts and only odd ones having high numbers of eggs per gram faeces. The combination of species among individual sheep was not constant, nor did there appear to be any regular succession of parasites throughout the flock. The average egg counts of **Haemonchus contortus** and **Ostertagia spp.** decreased in late autumn and early winter, but rose again in the spring, during early lactation, following which there was a drop in the averages by mid-summer. The average egg counts of **Cooperia curticei** did not fluctuate greatly during the experiment. Among other species, e.g. **S. papillosus** and the **Chabertia-Oesophagostomum** group, because egg counts were low, seasonal differences in intensity of parasitism were not clearly evident.

In some animals it was found that re-infection by **H. contortus, Ostertagia** spp. and **C. curticei** took place after the winter decline in parasitism. There was no evidence that parasitism by any species influenced the course of subsequent parasitism by the same or other species.

Throughout the experiment, with the exception of **Tr. ovis** and **Nematodirus** eggs of all species which normally occur abundantly in lambs were found in the faeces of some, at least, of the ewes, and therefore, the ewes were continuously acting as contaminating agents of pasture. No data were secured, however, on the extent to which these eggs were able to give rise to infective larvae.

PARASITISM IN LAMBS IN THE LIGHT OF THAT IN THEIR MOTHERS.

Using the same methods of study as in the previously described investigation experiments were taken a stage further by observing the extent to which parasitism developed in lambs, in the light of that which occurred in their mothers. The experimental sheep were kept as the sole inhabitants of one paddock and egg count data were collected at regular intervals from the time of birth of lambs until mid-summer.

Eggs of **Haemonchus contortus, Ostertagia** species (presumably **O. circumcincta** and **O. trifurcata), Strongyloides papillosus** and **Cooperia curticei** were identified in the faeces of the ewes. Among the lambs eggs of the following species were found:—**H. contorus, Ostertagia** spp. **S. papillosus, C. curticei, Nematodirus filicollis, N. spathiger, Trichuris ovis** and the group **Chabertia-Oesophagostomun.**

As in previous experiments, eggs of **Trichostrongylus** spp. could not be distinguished from those of **Ostertagia** spp., but for reasons previously given, the data are regarded as pertaining mainly, if not exclusively, to **Ostertagia.**

It is seen that the ewes were not a significant factor in contaminating pasture with **Nematodirus** eggs and it is concluded therefore, that **Nematodirus** immature stages were able to overwinter on the ground. In regard to **Trichuris ovis,** the writer believes that eggs of this species do not readily rise in ordinary flotation methods of faecal examination; doubt exists as to whether they were completely absent from ewe faeces, in the present experiment. However, in other experiments, using different technique, eggs of this species have either not been recovered from ewe faeces, or have been sporadically present in small numbers.

A noteworthy feature of parasitism in the lambs was the appearance of **S. papillosus** and **Ostertagia** spp. appreciably earlier than **H. contortus** and **C. curticei,** even though eggs of all four genera were being conveyed to the ground from the ewes from the beginning of the observations in numbers of the same order. The egg counts, for all species in the ewes, with the exception of **C. curticei** declined as mid-summer was approached, whereas in the lambs, egg counts progressively increased. It is reasonable to conclude that as mid-summer was approached the lambs contaminated pasture more so than the ewes and set in train a process of self-augmentation of parasitism.

The role of ewes as vectors of lamb parasites was investigated in another experiment. The course of parasitism in a small flock confined to one paddock, and allowed to increase naturally, was followed for a number of years. Faecal examination of egg numbers was regularly carried out.

It was apparent, for **H. contortus** and **Ostertagia** spp., that the ewes were able to contaminate pasture with eggs in large numbers, particularly during late summer-autumn, and to a lesser extent, during the lactation period. During winter, and again during late lactation and early summer, the egg counts in the ewes declined. As in other experiments it was found that ewes were not a factor as vectors of **Nematodirus** spp. and **Trichuris ovis and** the conclusion was reached that these species were able to overwinter on the ground in spite of any disinfecting effect through grazing of resistant sheep.

While the ewes were able to develop high egg counts, it did not necessarily follow that the lambs became heavily infected with worms, and it was concluded that factors of climate by inhibiting development of infective stages played an over-riding part in determining the course of parasitism in the lambs.

THE MODE OF BUILD UP OF PARASITISM

When parasitism is not overwhelming, the writer has found that there tends to be accumulation that culminates in a single peak of population for each species. Each species appears to be acquired over a relatively short period, perhaps a few weeks, during which time climate, mainly humidity and temperature in combination, brings about a step-like growth of populations. Resistance to super-infection then sets in and inhibits further increase in the population of a species. Subsequently over a variable period there is intermittent eliminaton of parasites. Under these conditions there does not appear to be rapid turnover of populations of parasites, in which there is a continuous and coincident process of acquisition and elimination of worms. It is possible, however, that resistance to parasitism resulting from previous infection may be short-lived and that a second period of parasitism, by the same species, may intervene. Possibly this happens with **Haemonchus** and **Ostertagia** and sometimes even with **Nematodirus** when there may be periods of spring and autumn acquired parasitism. **Trichostrongylus** would appear to have only one peak of parasitism. In regard to **C. curticei** the build of parasitism appears to continue over a longer period than for other species, since the writer has found this species in greatest numbers in sheep in their second year of life. So far as the rate at which parasites are acquired is concerned, it has been found for Manawatu conditions, that species of the first wave, **Ostertagia** spp., **Nematodirus** spp., and **Strongyloides papillosus,** do not accumulate rapidly enough in the spring to overwhelm lambs. Whether this is due to the populations of infective larvae that obtain in this district or to the speed with which resistance to superinfection is evoked, or to both, is not clear. In regard to autumn acquired parasitism, experiments have indicated that overwhelming populations of **Haemonchus** and **Cooperia curticei** may be acquired within two weeks. Under this degree of exposure to parasitism, a fortnightly, at least, anthelmintic programme would be necessary.

THE PROCESS OF PARASITE ELIMINATION

When conducting post mortem examinations on sheep in the autumn it not infrequently happens that populations of parasites are found in process of elimination. It is evident, in these instances, that while many parasites remain in their normal habitat, there is mass eliminaton of worms. In order to observe the process of elimination of worms more closely examination of the entire output of the faeces of one lamb was carried out over the first nine months of its life, search being made for adult worms. It was found that there was rhythmical elimination of parasites from the time the lamb reached about three months of age, in which periods of elimination for a number of species tended to be in unison. It would seem, under these circumstances, that some non-specific factor was superimposed on acquired resistance. What factor or factors that brought this about was not clear. Whatever factors were involved, it was apparent that they caused egg counts to drop, and associated with this drop worms were passed out. In regard to **Haemonchus** a fall in egg counts was associated with an immediate voiding of a portion of the population of parasites. With **Nematodirus,** however, following a fall in the egg count, a few days elapsed before worms were found in the faeces. It was noticeable, over short periods, that appetite, as measured by dry weight of faeces, had a three or four-day rhythm and associated with the rhythm there were fluctuations in the daily output of eggs and also elimination of parasites.

AVAILABILITY OF INFECTIVE LARVAE THROUGHOUT THE YEAR

In order to discover to what extent infective larvae were available to sheep at different seasons of the year a number of experiments were carried out. Lambs were reared indoors free of parasitisms (except **Strongyloides)** and portions of the flock exposed to parasitism in the field on different dates; other experiments made use of lambs born out of season and exposing them to parasitism in the field. It was found that all species of nematodes parasites could be acquired by previously uninfected sheep throughout the year, though during late autumn and winter smaller populations were acquired than at other seasons. The infective potential of **Nematodirus** spp., **Trichuris,** and **Trichostrongylus** spp. appeared to be maintained at a higher level than other species during the winter. In regard to **Ostertagia** the fact that this genus is able to accumulate in large numbers in early spring would indicate that it is able to survive under cool conditions on the ground; however,, data shows that its infective potential during winter was at a lower level than for the previously mentioned species.

DATE OF LAMBING AND INTENSITY OF PARASITES

Data secured on this aspect of the worm problem showed that fluctuations in the date of spring lambing within the period August, September and early October did not appear to have significant bearing on the intensity of parasitism or on the ensuing succession of parasites. When lambing occurred well outside this period parasitism took a different course; very late born lambs, as late as mid-summer, tended to acquire overwhelming parasitism, particularly by **Haemonchus.** The writer believes that lambs born very early also develop a different epidemiological picture; under these conditions in the warmer parts of New Zealand species such as **Haemonchus** have two seasons of parasitism, spring infection and then autumn infection; the spring infection tends to involve smaller populations of the parasite and the evidence is that such small infections have a protective effect when lambs are exposed to autumn **Haemonchus** parasitism.

THE EXTENT THAT THE EPIDEMIOLOGICAL PICTURE FLUCTUATED IN A DISTRICT IN THE SAME SEASON.

The course of parasitism in two flocks maintained in neighbouring paddocks was followed by means of regular egg counts. It was found that while parasitism in one flock increased to a higher level than in the other, the average fluctuations in the egg counts moved coincidently in the same direction. The main fluctuations in the average counts were during the summer and early autumn and were correlated with periods of rain. That is, whatever the initial differences in degree of exposure of the two flocks to infective larvae, and whatever their relative susceptibility, the course of summer and autumn parasitism presented similar features which appeared to be influenced by periods of rain.

RESERVOIR HOSTS

Previously reference has been made to the range of species that have been found in sheep. Of this list the following are normally cattle parasites:—

Cooperia oncophora	**Nematodirus helvetianus**
Cooperia mcmasteri	**Nematodirus abnormalis**
Cooperia punctata	**Ostertagia ostertagi**

and one species is a goat parasite, **Trichostrongylus capricola.** The writer has found that the above-mentioned **Cooperia** spp. and **Ostertagia ostertagi** occur in sheep only when they are in close association with cattle and that, when the association is broken, they disappear from the sheep. A similar state of affairs apparently holds for **T. capricola.**

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Discussion on Mr. Tetley s Paper

Mr. WHITTEN: Is the spring rise in egg count due to an increased egg production of worms already present or is it due to a fresh infection? I am very intrigued by the spontaneous elimination of the parasites. The term " self-cure" was used by Stoll for this phenomenon which he observed in infested sheep. While I was working in Northern New South Wales, we observed self-cure occurring simultaneously in practically every sheep in a flock of about 30 animals. Later it was shown that infestations of different ages were eliminated at the same time in different animals. More recent work at the McMaster laboratory has shown that a dose of larvae may stimulate a transient immune reaction which results in the elimination of adult worms but the larvae responsible for the stimulation may establish themselves and may set up a fatal infestation. Might not the simultaneous elimination of different species be due to a group reaction Stewart's recent work has shown that many nematodes contain a similar if not identical lipid and it is this that is involved in his complement fixation test.

Mr. TETLEY: In reply to your first question I think both factors are involved in the spring rise in egg count. With reference to self-cure, this was a term proposed in the days when helminth immunity was considered to be quite different from bacterial immunity. Later work showed that the two were similar and that in the case of the helminths, precipitates resulting from the antibodies caused mechanical interference with the functions of the worms. In my sheep the elimination of the worms was partially correlated with the rhythm in faecal output and therefore there appears to have been some non-specific factor or factors involved as well as acquired resistance.