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THE EPIZOOTIOLOGY OF HELMINTH INFESTATION IN SHEEP IN THE SOUTH-WESTERN DISTRICTS OF THE CAPE*

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INTRODUCTION

The production of wool and mutton has not kept pace with the phenomenal expansion which has characterized the other sectors of the agricultural and industrial economy of the Republic of South Africa. The lag in production can be attributed to seasonal fluctuations of both quantity and quality of the pastures, mainly as the result of variability of the climate. It is essential that the unit production of wool and mutton be increased, despite the poor grazing available; yet the most important factor militating against efficient feed conversion and, therefore, increased production, is helminth infestation.

In young growing animals a worm infestation can result in stunted growth which may be permanent, even though the infestation may have been eliminated. As stated by Hammond (1932) " A check in growth received early in life affects the ultimate size of the animal ". Sheep are rarely parasitized by only a single helminth species; helminthiasis in sheep is usually the result of a combined assault of numerous genera occurring in varying numbers, each contributing to the disease syndrome. Moderate numbers of parasites adversely affect growth and productivity; heavier worm burdens cause marked clinical symptoms or even death of the host. Scientific methods of control in South Africa have, hitherto, been hampered by a lack of knowledge of the epizootiology of these parasites.

A study of the epizootiology necessitates an intimate knowledge of the life-cycles, ecology and host-parasite relationships. The important facets of the life-cycles have been well described by Gordon (1953, 1958). Excellent reviews of the ecology have been published by Crofton (1963) and Levine (1963) and of the host-parasite relationships by Urquhart, Jarrett & Mulligan (1962) and Soulsby (1965a). Most recently a very comprehensive, and well documented review on the helminth transmission in domesticated animals, especially on the ecological aspects, has been published by Kates (1965).

In attempts to establish the epizootiology, the seasonal incidence of parasites has been surveyed by the collection of faecal samples at regular intervals and by doing differential worm egg counts (Gordon, 1948; Tetley, 1949; Crofton, 1954; Meldal-Johnsen, 1961; Rossiter, 1961, 1964; Barrow, 1964; Muller, 1964).

The survey conducted by Muller (1964) at Outeniqua in the South Western Cape, although indicating certain trends, was not satisfactory as it did not give a complete definition of the epizootiology of the parasites involved. Furthermore, the number of faecal worm eggs is not always an indication of the degree of infestation; although high faecal egg counts may indicate a heavy infestation in young animals, the opposite may be found in adults, where low egg counts can be encountered, despite relatively heavy parasitic burdens. The validity of this method of determining the worm burdens has been doubted by various authors (Gordon, 1948; Tetley, 1949; Crofton, 1954; Muller, 1961; Reinecke, 1963).

The following authors have determined that surveys of the epizootiology are best carried out by slaughtering members of a flock at regular intervals and counting and identifying the worms *post mortem* on a more critical basis: Tetley (1949), Morgan, Parnell & Rayski (1951), Parnell (1962), Barrow (1964), Rossiter (1964), Viljoen (1964) and Dunsmore (1965).

Attempts were made to correlate the ecology of the free-living stages with the worm burdens in animals continually exposed to infestation from birth until they were adults.

It was decided to carry out a comprehensive experiment, in which sheep would be slaughtered at regular intervals, and doing total and differential worm counts, at autopsy. Worm-free lambs would be exposed to pasture for four weeks to determine the availability of viable, infective larvae. Simultaneously, two grazing flocks, one composed of lambs and the other, yearlings and adults, would be examined.

Materials and Methods

Location

The experiments were carried out at the Outeniqua Experimental Farm, Latitude 34° 0′ S, Longitude 22° 25′ E, in the district of George, Cape Province. The farm is situated approximately six miles from the sea in close proximity to the Outeniqua mountains, which rise to a height of 1,000 metres above sea level.

Climatic conditions

The rainfall is non-seasonal and averages 820 mm (32·28 inches) per annum, while fog and sea-mists are common during the cooler months of the year. The driest months are January and July. The climate is temperate, and daily temperatures fluctuate but slightly, while frost is very rare.

Daily variations in the climatic conditions were recorded throughout the experimental period (See Appendix, Table 1).

Grazing

The pastures on the farm are permanent grass-clover leys, with alternate grazing provided in winter by annual cereal and fodder crops, i.e. oats and lupins (*Lupinus* spp.), which had been established at least three months previously.

On 1 July 1961 all the animals in the experiments were rotated on these alternate pastures, which were utilized for the first time as follows:

(*a*) 1 to 7 July on lupins;

(*b*) 8 to 17 July on oats;

(*c*) 18 and 19 July on Kikuyu (*Pennisetum clandestinum*);

(*d*) 20 July to 3 August back to the lupins;

(*e*) 4 to 16 August back to the oats;

and thereafter the whole flock was returned to the permanent grass-clover leys.

The rotation of the flocks on the pastures was primarily governed by the state of the grazing in the camps and frequent rotation of the flocks on the pastures was an essential feature of the normal husbandry. This is illustrated by the flock movements specified above.

Sheep

Pure-bred German Merinos were used and divided into three flocks as follows:

Group A—" Indicator " Lambs:

Sixty-five lambs were born and housed on concrete floors which were regularly cleaned and fed hay free of infective larvae. These worm-free lambs were placed on pasture when required.

Group B—Lambs:

Fifty-four lambs, born and reared on pastures.

Group C—Yearlings and Adults:

Seventy-three ewes and wethers grazing on pastures.

All animals were individually numbered by means of ear tags. Groups B and C were treated with 4 ml of 50 per cent carbon tetrachloride in peanut oil, intramuscularly, against *Fasciola hepatica* Linnaeus, 1758, on 3 February and 13 April 1961, respectively, because of severe infestation of *F. hepatica* experienced during the previous year.

Stocking rate

The average stocking rate on all pastures was six animals per acre, and this was maintained throughout the experiment by the addition of other sheep to the flock as the experimental animals were slaughtered. A herd of Jersey cattle sporadically grazed some of the pastures used in these experiments.

All the sheep on the farm had to be penned at night to protect them against marauding dogs, and were returned to the pastures in the early morning (7 a.m.).

Necropsy procedure

Animals from each group were slaughtered simultaneously, the gastro-intestinal tract removed, and worms recovered according to the procedures described by Reinecke (1961).

Identification of larval stages was made according to the descriptions of Veglia (1915), Andrews (1939), Threlkeld (1948), Basir (1950), Kates & Turner (1955) and Douvres (1956, 1957a, b). Larvae in the third moult and fourth stage were classified as fourth stage larvae; those in the fourth moult and fifth stage were, together with adults, regarded as adult worms.

Adults were identified according to the descriptions of Yamaguti (1961). Where large numbers of worms of the same genus were present 60 to 100 adult males were identified and the number of each species estimated from this analysis. Females in these cases were identified on a generic basis only.

Graphs

The total number of worms recovered was divided by that of the autopsies completed during any particular month. These averages were converted to logarithms and used to plot the monthly variations in worm burdens illustrated in the graphs.

Experimental Observations

The experiments were commenced on 26 April 1960, and were concluded on 13 September 1961. Data are summarized in tables in the appendix, and presented graphically in the text.

The following species of helminths were identified:—

Trichostrongylus colubriformis (Giles, 1892)
Trichostrongylus falculatus Ransom, 1911
Trichostrongylus axei (Cobbold, 1879)
Trichostrongylus vitrinus Looss, 1905
Trichostrongylus pietersei le Roux, 1932
Trichostrongylus rugatus Mönnig, 1925
Ostertagia circumcincta (Stadelmann, 1894)
Ostertagia trifurcata Ransom, 1907
Ostertagia ostertagi (Stiles, 1892)
Haemonchus contortus (Rudolphi, 1803)
Cooperia curticei (Giles, 1892) emend. Railliet, 1893
Cooperia pectinata Ransom, 1907
Cooperia punctata (v. Linstow, 1906)
Cooperia spatulata Bayliss, 1938
Nematodirus spathiger (Railliet, 1896)
Nematodirus filicollis (Rudolphi, 1802)
Bunostomum trigonocephalum (Rudolphi, 1808)
Oesophagostomum venulosum (Rudolphi, 1809)
Chabertia ovina (Fabricius, 1788)
Trichuris globulosa (v. Linstow, 1901)
Trichuris parvispiculum Ortlepp, 1937
Strongyloides papillosus (Wedl, 1856)

The authors quoted are according to Yamaguti (1961). The species *Haemonchus contortus* and *Cooperia curticei* are, however, spelt in the conventional manner.

Group A—" Indicator " Lambs

Two methods for the determination of pasture infestation have been used in the past:

(i) The determination of faecal egg counts, implying that variations in egg counts would indicate the fluctuations in pasture infestation (Crofton, 1963).

(ii) The quantitative analysis of the free-living stages on the pasture itself (Taylor, 1939; Crofton, 1948, 1949).

Examination of the herbage does not indicate whether:—

(*a*) the larvae present on the herbage will be ingested by the grazing sheep;

(*b*) the larvae are viable, i.e. capable of developing to adult worms.

To overcome these obstacles, the use of worm-free lambs allowed to graze for limited periods on infested pastures, will show whether infective larvae are available *and* viable.

These animals will be referred to as " Indicator " lambs.

Materials and Methods

Sixty-five lambs born, raised and maintained worm-free were used. They were placed on infested pastures together with the animals of Groups B and C as follows:

Three lambs were placed on the pastures every fortnight as from 3 August 1960, and two of the three were slaughtered after 14 days. The surviving member of each group was killed after four weeks at pasture. The age of the first group was approximately 10 weeks. The lambs used in these experiments, having been reared indoors, did not immediately adapt themselves to a grazing habit when introduced to the pastures, and few worms were acquired within 14 days. Consequently, the procedure was altered from 21 December 1960, and two lambs were placed on pasture every 14 days and killed four weeks later. At the conclusion of the experiment on 13 September 1961, the last lambs slaughtered were 18 months old (see Fig. 1).

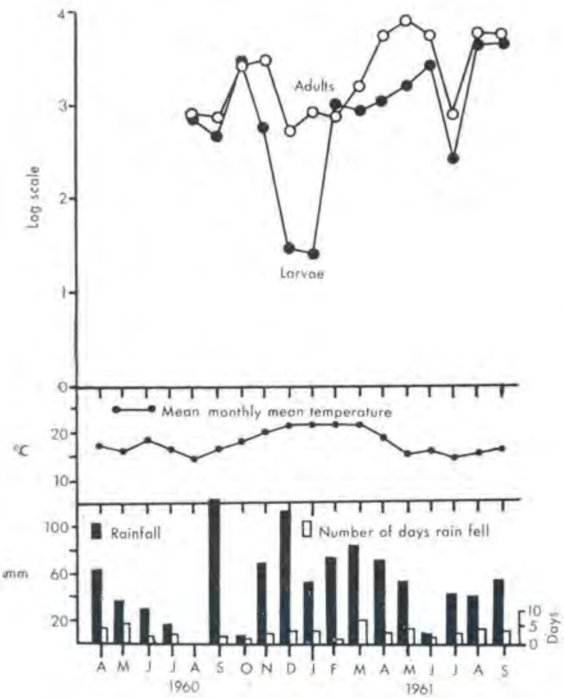

FIG. 1, Group A.—Monthly variations in worm burdens Ordinate = worms recovered log scale Abscissa = months

Results

Worms recovered *post mortem* are summarized in Appendix Table 2 and illustrated in Fig. 1. The entire intestinal contents of two animals (K6026 and K6034) were accidentally discarded.

Total worm burdens

There was a decrease in numbers recovered from August to September, followed by a medium peak in October; after which there was a downward trend starting in November and terminating in February. From the middle of February worm counts rose fairly rapidly to culminate in a major peak at the beginning of May, with a tendency to decline from the middle of May, falling precipitously in July, following the drafting of the flocks to the new pastures. Counts started to rise from the end of July to reach another peak in August, equalling the June counts; thereafter, declining in September.

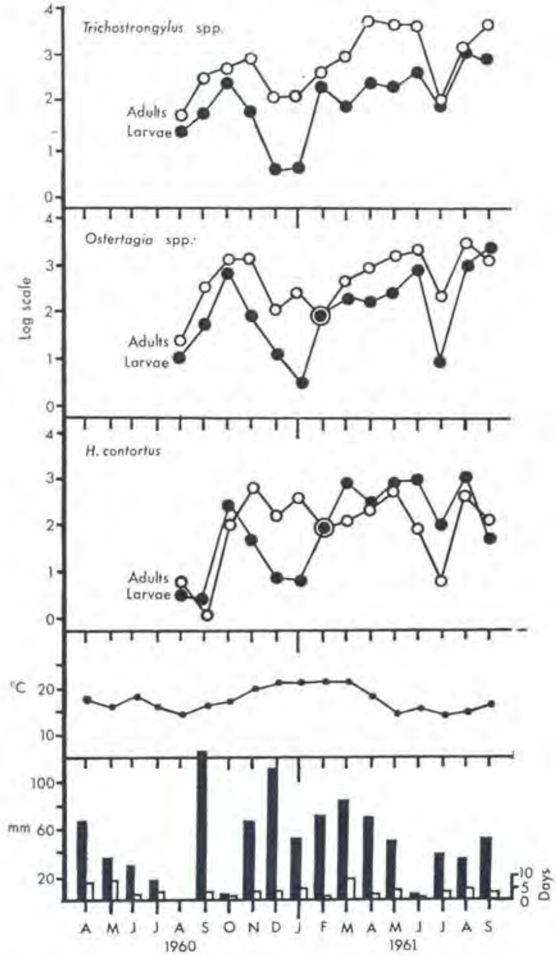

FIG. 2, Group A.—Fluctuations in major genera

Major genera

Trichostrongylus spp.: This genus followed the general trend of the total worm burden throughout the period, except that the counts increased from August to September 1961. The dominant species were *Trichostrongylus colubriformis* and

T. falculatus. Except for a deviation from the general trend in spring, *T. colubriformis* accounted for the majority of worms recovered for the rest of the period. *T. falculatus* reached its major peak in April, declining steadily thereafter to September 1961. *T. axei* was entirely absent from the end of November to March and only present in moderate numbers during the rest of the survey period. *T. pietersei* was erratically recovered from October to December, being recorded in four out of 14 animals, and was completely absent until March; thereafter, except in the case of four sheep, it was consistently recovered. *T. vitrinus* was recovered from the majority of sheep during the period April to September 1961, but it was almost entirely absent during the preceding summer. *T. rugatus* was recorded from one sheep only (6022), killed on 9 May 1961, when 59 worms were recovered.

Ostertagia spp.: Trends were similar to those of the total worm burden with minor peaks in October 1960 and June 1961, and a major peak in August and September 1961. Numerically, *Ostertagia circumcincta* was the dominant species. *O. trifurcata*, except in two sheep, was consistently recovered in moderate numbers from March to September 1961, whereas it was erratically present in small numbers during the preceding period. *O. ostertagi* was absent in all specimens except in those of seven sheep until the end of July; thereafter, with one exception, it was consistently present in moderate numbers during August and September.

Haemonchus contortus: The general trend was similar to that of the total worm burden. During January, this species was more prevalent than other species, thereafter receding to lesser prominence. There were major peaks in May and June; and following the July decline, the counts rose to a further peak in August.

Minor genera

Cooperia spp.: These were either absent, or recovered erratically from individual sheep until March; thereafter, they were consistently present in low numbers, reaching a peak in May.

The order of prevalence of the species was *Cooperia curticei*, *C. punctata*, *C. pectinata* and *C. spatulata*, being recovered from 31, 14, 12 and 11 lambs respectively.

Nematodirus spp.: These were either absent or present in individual sheep only, until March 1961; thereafter, they were recovered from the majority of lambs in June, August and September. *Nematodirus spathiger* was recovered in larger numbers than *N. filicollis*.

Bunostomum trigonocephalum: This species was recorded in nine sheep at extremely erratic intervals, usually as fourth stage larvae, and in two sheep as adults (Appendix Table 2).

Oesophagostomum venulosum: Except in nine sheep, this parasite was absent until March; thereafter, with five exceptions, it was consistently recovered from all sheep.

Trichuris spp.: These were rarely present; seven lambs had *Trichuris globulosa* and two had *T. parvispiculum*.

Strongyloides papillosus was of no apparent importance, being recovered only from seven sheep.

Comment

Large numbers of infective larvae were available on pastures during the cool months from April to September, when the mean monthly mean temperatures varied from 14·6° to 18·2° C. The precipitous fall in worm burdens in July 1961, was the result of the change to the new pastures, grazed for the first time. The recoveries during the latter half of August, however, indicated not only a heavy contamination of, but also extremely favourable conditions for the development of large numbers of infective larvae on these pastures. When temperatures exceeded 21° C, i.e. during the months of December to February, the lowest numbers of worms were recovered. The only exception was the minor peak of *H. contortus* in January.

The following features in the incidence of the major genera were noted:—

(i) From August to November the numbers of *Trichostrongylus* spp. and *Ostertagia* spp. recovered, exceeded those of *H. contortus*, in all probability the result of the cool weather, which is more favourable for *Trichostrongylus* spp. and *Ostertagia* spp. (Mönnig, 1930; Rogers, 1940; Dinaberg, 1944a, b; Gordon, 1948, 1950, 1953, 1958).

(ii) *Ostertagia* spp. exceeded *Trichostrongylus* spp. from September to January in the warmer, moister weather, when the climatic conditions were apparently *more* favourable for *Ostertagia* spp.

(iii) Despite the fact that temperature and moisture requirements were extremely favourable for the development of *H. contortus* in summer (November to March) according to Dinaberg (1944a, b), they were only recovered in relatively large numbers in January. The relative paucity of *H. contortus* in summer, in contradistinction to its abundance in winter, cannot be accounted for at this stage.

(iv) Both *Ostertagia* spp. and *H. contortus* showed a precipitous drop during July, with an equallly rapid increase in August and September. The recoveries of *Trichostrongylus* spp. did not show these tendencies.

With the exception of four months (October 1960, June, July and August 1961) the monthly rainfall was in excess of 50 mm (Appendix Table 1). Thus for the major part of the experimental period, the moisture requirements of the free-living stages were satisfied (Crofton, 1963; Levine, 1963).

The graphs of the major genera (Fig. 2) show the following salient features:

(i) *Trichostrongylus* spp.: Throughout the period, the number of adults recovered always exceeded the number of larvae. This pattern was followed at the time of low recoveries during summer, when the climate was unfavourable for this genus, as well as in the cooler period for the remainder of the year.

(ii) *Ostertagia* spp. followed trends similar to those of *Trichostrongylus* spp. in respect of the relative proportions between larvae and adults during the summer months. During the winter period, however, there was a greater accumulation of fourth stage larvae.

(iii) *H. contortus.*: The ratio of larvae to adults followed the trends of the previous two genera up to February, with adults predominant. From the end of February, however, there was a complete reversal of the proportions of larvae to adults, the former exceeding the latter by far.

Group B—Lambs

Previous investigations regarding the course of infestations in lambs under field conditions, have been followed by slaughtering lambs regularly, and carrying out total and differential worm counts (Tetley, 1949; Morgan *et al.*, 1951; Parnell, Rayski, Dunn & McIntosh, 1954; Hovorka & Dedina, 1961; Parnell, 1962; Brunsden, 1963).

The present experiment was set up to ascertain the variation in worm burdens in lambs, born and reared on pastures. Observations were carried out on sheep from three to 15 months of age. To avoid confusion even the oldest sheep in this group are referred to as lambs.

Materials and methods

Fifty-four lambs, born between 28 June and 3 August 1960, grazed with the yearlings and adults (Group C). Every two weeks, two lambs were slaughtered for worm counts at autopsy, commencing on 15 September 1960 and concluding on 31 August 1961 (see Fig. 3).

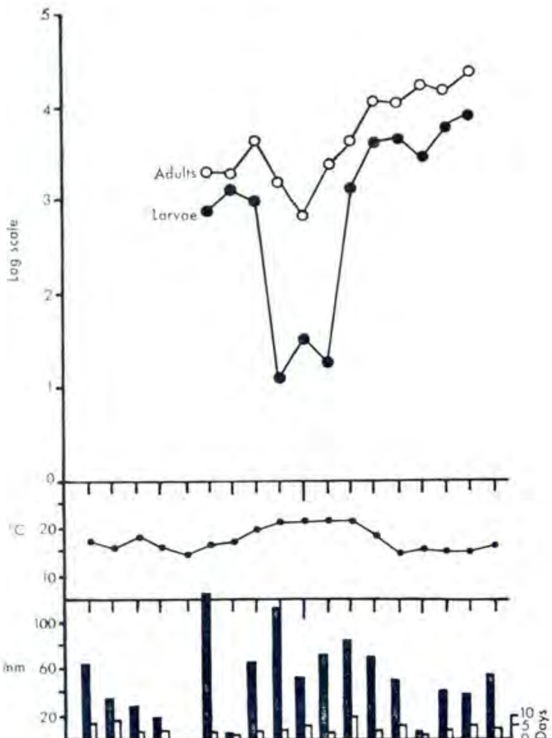

FIG. 3, Group B.—Monthly variations in worm burdens

Results

The numbers of parasites recovered at autopsy are recorded in Appendix Table 3, and illustrated in Fig. 3. Specimens from three sheep (K6015, K6017 and K6024) were accidentally discarded.

Total worm burdens

From September to January, worm burdens declined, and then rose steadily, with minor fluctuations, to a major peak in August.

The drafting of this flock to the new pastures on 1 July had little effect on the number of worms recovered.

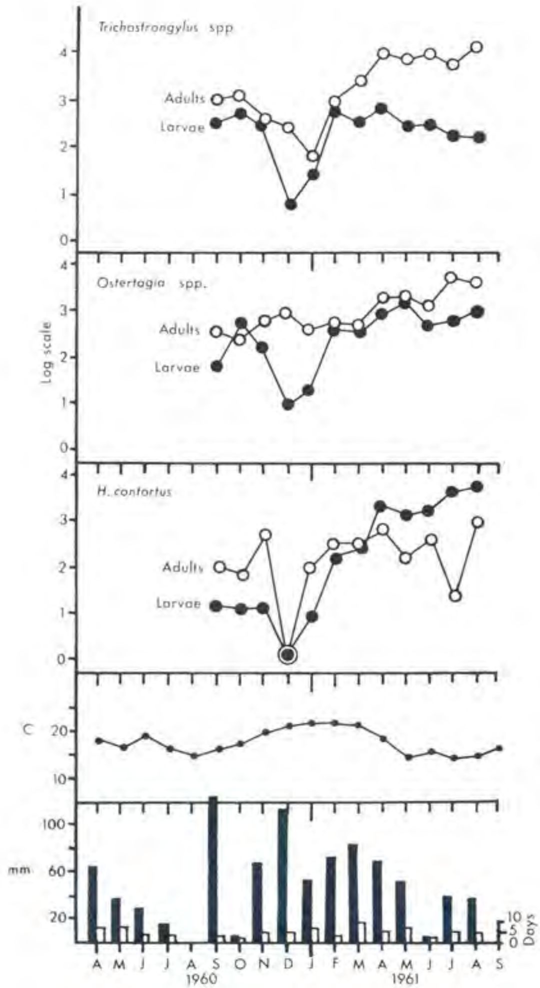

Fig. 4, Group B.—Fluctuations in major genera

Major genera

Trichostrongylus spp.: This was the dominant genus and the counts followed the same general trend of the total worm burdens, apart from a minor depression in July (Fig. 4).

The fluctuations during the months of June and July were the result of high burdens in individual sheep. The peak in August 1961, however, was the result of heavy infestations in all the sheep slaughtered, worm burdens ranging from 12,511 to 30,627, with an average of 21,104. Except in the case of three sheep, from which no larvae were recovered, fourth stage larvae were present in moderate numbers throughout (Appendix Table 3).

Although more fourth stage larvae than adults were recovered from a few sheep for a short period from January to mid-March, adults were dominant for the rest of the survey, particularly from April to the end of August.

In the course of the differential worm counts, two distinct types of *Trichostrongylus* spp. were noticed:—

(*a*) Small, pale, immature worms;

(*b*) larger, sexually mature worms.

A number of these adolescent *Trichostrongylus* spp. were selected at random from the ingesta of 16 animals, slaughtered from April to August, and examined microscopically. The results are summarized in Appendix Table 5.

The immature females were either barren, or had few eggs in the uteri (ranging from two to nine, with a mean of five), whereas the adult females, by comparison, had well developed uteri, filled with eggs in all stages of maturation, averaging 120 (ranging from 80 to 210).

In the males on the other hand, the testes of the immature specimens were underdeveloped with little or no pigmentation, while the mature males had well developed, darkly pigmented testes. In all cases the spicules were well developed and differentiated.

The number of immature *Trichostrongylus* spp. in Group B constituted 42·6 per cent of the total worms, while those in Group A averaged only 33·7 per cent (see Appendix Table 5). It was noted that in autumn and winter, in Groups A and B, the females outnumbered the males in both the mature and the immature forms of *Trichostrongylus* spp. The significance of this phenomenon is not clear.

T. colubriformis was the dominant species. *T. axei* was recovered in moderate numbers from 41 sheep, while *T. falculatus* was present in larger numbers in 37 sheep. *T. pietersei* and *T. vitrinus* were recovered erratically during most of the summer months until the middle of March. Thereafter they were fairly consistently recorded in reasonably large numbers from the middle of March to the end of August 1961. The latter two species appear to be winter parasites.

Ostertagia spp.: There was a slight rise in November, with a decline in counts over the rest of the summer months, followed by a steady rise to a major peak in August.

Except for the period November to January, the recoveries of larvae closely followed those of the adults. The low recoveries of larvae in summer were similar to the trends of *Trichostrongylus* spp. larvae. During the period September to January, no larvae were recovered from five sheep; but were present in all the other sheep necropsied, and in 18 out of 50 sheep, larval recoveries outnumbered the adults.

O. circumcincta was the dominant species and was consistently present, while *O. trifurcata* was recovered from most necropsies in moderate numbers. *O. ostertagi* was recorded in only nine sheep.

Haemonchus contortus: Recoveries of this parasite rose to a minor peak in November. In December, however, the numbers recovered were completely insignificant; of the three lambs slaughtered, one had only seven worms, while the other two had no worms. These negative recoveries were surprising in view of the fact that in November and December the mean monthly mean temperatures were 19·9° and 21·3° C, and a monthly rainfall of 66·5 mm and 113 mm respectively, was recorded. Thereafter, worm counts rose steadily throughout the rest of summer, autumn and winter to reach a peak in August.

In the majority of necropsies both larvae and adults were present. In 24 instances, from the middle of March to the end of August, there were more larvae than adults; in two, the adults exceeded the larvae; in six, only larvae were recovered.

Attention must be drawn to the fact that from March onwards, the high total counts of *H. contortus* were largely the result of the preponderance of fourth stage larvae.

Minor genera

Nematodirus spp.: Both *Nematodirus spathiger* and *N. filicollis* were recorded sporadically throughout the whole period. With few exceptions, fourth stage larvae were always present. Approximately 71 per cent of the larvae were *N. spathiger* while the remaining 29 per cent were *N. fillicollis*. From April to August 1961 when the animals were approximately a year old, significantly greater numbers of *Nematodirus* spp. were recorded than in the preceding months.

Cooperia spp.: This genus was recorded in 25 lambs only, and no significant trends were noted. Larvae were recovered from 15 sheep. The order of prevalence of adult worms was *Cooperia curticei, C. punctata* and *C. spatulata*. In only one instance was *C. pectinata* recorded.

Bunostomum trigonocephalum: Adults were recovered from most sheep in moderate numbers, varying from 1 to 80. Fourth stage larvae were recorded in four sheep, ranging in numbers from 18 to 142.

Oesophagostomum venulosum: Except in the case of 10 sheep, adults were consistently recovered at all autopsies in numbers varying from 1 to 68. In five lambs fourth stage larvae were recorded in numbers ranging from 10 to 78.

Chabertia ovina: With few exceptions, adults were consistently present and recovered in numbers varying from 1 to 194; while from 5 to 45 larvae were recovered from four sheep.

Trichuris spp.: Twenty-eight sheep were infested, 13 with *Trichuris parvispiculum* and 10 with *T. globulosa*. No mixed infestations were recorded. In each case only one of the two species was present.

Strongyloides papillosus: This was recovered from six sheep, in numbers varying from 9 to 211.

With the exception of *Nematodirus* spp. (*vide supra*) the minor genera showed no obvious seasonal fluctuations.

Examination of the caecal and colonic ingesta invariably showed either whole or " ghost " forms of parasites, normally found in either the abomasum or small intestine.

Comment

In view of the fact that relatively few infective larvae were present on the pastures (see " Indicator " lambs), the small numbers of parasites recovered during the period from mid-November to the end of January were not surprising, the only parasite occurring in reasonable numbers being *Ostertagia* spp.

The change of pastures on 1 July, which resulted in the precipitous drop in parasite recoveries in the " Indicator " lambs, had no such effect on the recoveries in Group B. The numbers recovered were in fact disproportionately large, especially in August. This phenomenon was largely due to the accumulation of fourth stage larvae of *H. contortus*.

Having determined the seasonal variations of worm burdens in lambs, it was deemed advisable to ascertain the worm burdens in older sheep, in order to compare their reactions with those of lambs, when exposed to the same degree of infestation.

Group C—Yearlings and adults

In the past, various workers in New Zealand, Scotland and South Africa have carried out critical slaughter experiments to determine the variations in worm burdens in yearling and adult sheep (Tetley, 1949; Morgan *et al.*, 1951; Wilson, Morgan, Parnell & Rayski, 1953; Barrow, 1964; Rossiter, 1964; Viljoen, 1964).

The present experiment was set up to determine the worm burdens of older sheep when exposed to continual infestation, and to compare these results with those of lambs born on the pastures.

Materials and methods

Seventy-three ewes and wethers were used. The experiment was commenced on 26 April 1960, and was concluded on 30 August 1961. Animals slaughtered up to mid-September were two years old. From then on until the end of August 1961, animals born in August and September 1959, were used.

With the exception of one group, when three animals were included, two animals were slaughtered every two weeks.

Results

The worm burdens are recorded in Appendix Table 4 and illustrated graphically in Fig. 5. Specimens from four sheep (813, 0933, 5921 and 0942) were accidentally discarded.

Total worm burdens

During 1960 worm burdens fell rapidly from April to July, rising thereafter to a peak in October. The number of worms recovered subsequently declined to a low level in January; rose to a peak in May, and then declined until the end of the period (August 1961).

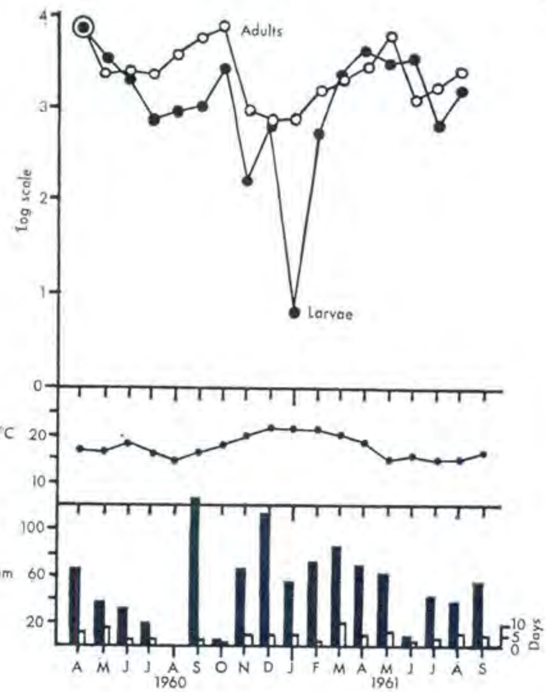

FIG. 5, Group C.—Monthly variations in worm burdens

Major genera

Trichostrongylus spp.: This genus decreased slightly in numbers from April to May 1960, and then increased to September and October. Subsequently there was a sharp drop to February, followed by a marked increase which lasted to April, with a tendency to decline in numbers until August.

Trichostrongylus axei was numerically dominant, and together with *T. colubriformis* was largely responsible for the peaks, while *T. falculatus* also contributed to the rise in October. The other species were not consistently recovered.

With the exception of the three months, April to June 1960, larval recoveries never exceeded the number of adults.

Ostertagia spp.: The pronounced depression, from April to July 1960, could be ascribed to the fact that only two out of the four sheep killed in July were infested. Thereafter infestation was recorded in all animals reaching a peak in October. The subsequent fall in summer and the rise in autumn and winter were not as pronounced as the tendencies in *Trichostrongylus* spp. It should be noted, however, that more *Ostertagia* spp. than *Trichostrongylus* spp. were recovered in February and March.

Haemonchus contortus: Of the 21 two-year old sheep slaughtered from April to the end of September 1960, only six showed but a light infestation (Appendix Table 5). Four out of the six sheep slaughtered during the period from September to October, which were just over one year old, showed consistent infestations, thus accounting for the minor peak in October. Decreased recoveries were recorded in November and December. Thence, worm burdens increased steadily until May 1961, to fall subsequently.

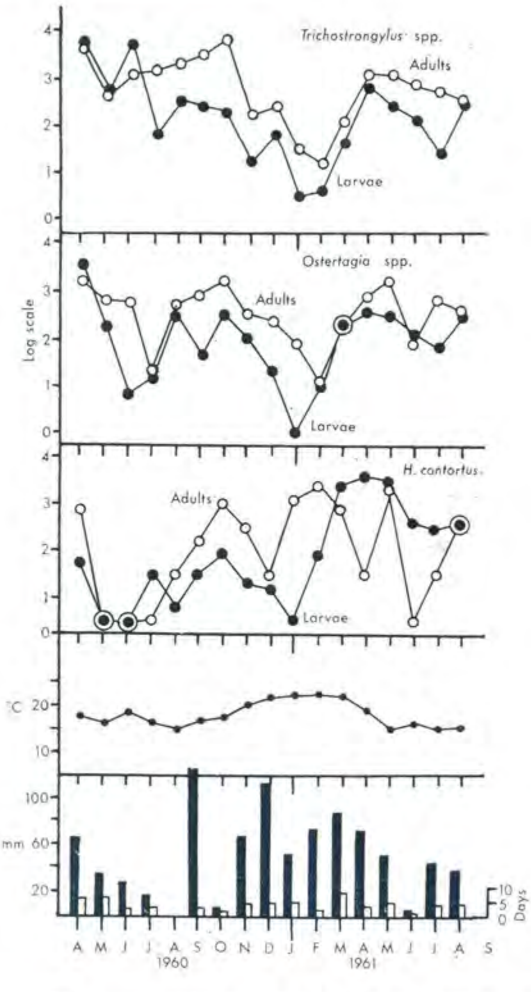

FIG. 6, Group C.—Fluctuations in major genera

Those animals slaughtered from May to August of 1960 and 1961 respectively, were of equivalent ages, yet the decline in *H. contortus* counts in 1961 was not as spectacular as in 1960.

The increasing worm burdens from March to May in 1961 was mainly due to the large numbers of fourth stage larvae recovered from March onwards.

Minor genera

Cooperia spp.: One third of the sheep slaughtered were negative for this genus. No seasonal trends were noted. Fourth stage larvae were found at 21 necropsies. Adult *Cooperia curticei* were recorded in 41, *C. punctata* in 10, *C. spatulata* in 10 and *C. pectinata* in 6 animals.

Nematodirus spp.: Adult worms were recovered from 11 sheep only, *N. spathiger* in 8, while the remaining 3 had *N. filicollis*. Fourth stage larvae, however, were recovered at 49 necropsies, the heaviest burdens being recorded from mid-March to August 1961.

Seventeen necropsies were negative for this genus.

Bunostomum trigonocephalum: Most animals had adult parasites ranging in numbers from 1 to 103. Larvae were recovered from 4 sheep, the numbers varying from 4 to 26.

Oesophagostomum venulosum: These were present in numbers varying from 1 to 131 adults, and larvae from 1 to 312. Forty-one autopsies were negative.

Chabertia ovina: Slightly more than half the animals were infested. Adult worms ranged in numbers from 1 to 84; while the numbers of fourth stage larvae ranged from 30 to 50.

Trichuris spp.: *Trichuris globulosa* was recorded in 20 sheep, *T. parvispiculum* in 8. No larvae were recovered.

Strongyloides papillosus: Although only 17 sheep were infested, worm burdens were generally higher than those recorded in Groups A and B.

Whole, partly degenerated, or " ghost " forms of various genera, normally present in the abomasum or small intestine, were consistently recovered from the ingesta of the caecum and colon.

Comment

Climatic conditions during the period April to August 1960, were unfavourable, with a decreasing rainfall from April onwards, culminating in an absolutely dry August. Temperature variations were considerable (Appendix Table 1). This arid, relatively warm period was probably responsible for the low worm counts recorded, particularly of *H. contortus* and, to a lesser extent, of *Ostertagia* spp. There was, however, hardly any appreciable effect on the numbers of *Trichostrongylus* spp. recovered.

By contrast, during the winter of 1961, when the rainfall recorded was within the normal range and the temperatures lower, no marked dissimilarity amongst the three genera was noted.

During the summer months, the numbers of *Trichostrongylus* spp. and *Ostertagia* spp. showed a general decline, particularly from October to February, while *H. contortus* decreased during the period October to December, but recovered rapidly thereafter. During the period January to April 1961, the total recoveries of *H. contortus* exceeded those of the other genera.

The high incidence of *T. axei* in this group, and also in the older animals of Group B, when compared with that of the younger animals slaughtered early in the experiment, indicates that the older animals are more prone to infestation with this species and, conversely, are less prone to infestation with *T. colubriformis* (Tetley, 1949) (see Fig. 7).

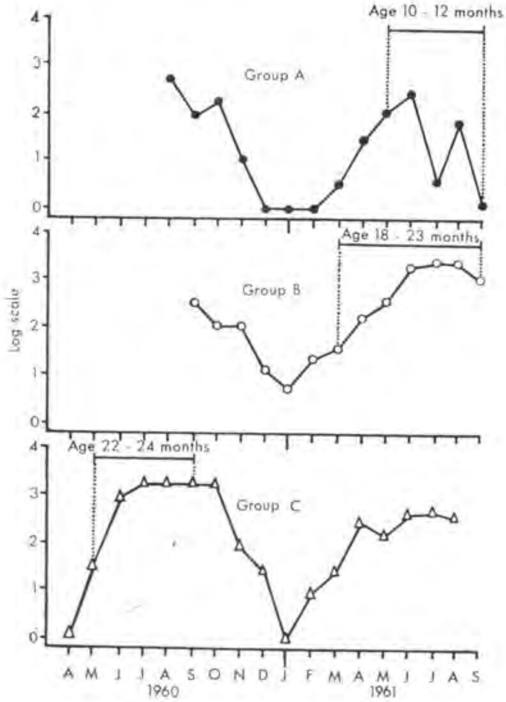

FIG.7.—Age incidence of *T. axei* in Groups A, B and C

DISCUSSION

The large variety of worm species encountered at Outeniqua, complicates the study of the epizootiology and, for the sake of convenience, this discussion is dealt with under the following separate headings:—

(i) Ecology of the free-living stages,

(ii) Parasitic stages in the specific host.

(i) *Ecology of the free-living stages*

Many workers have studied the ecology of the free-living stages, and their work has recently been reviewed by Levine (1963), Crofton (1963), Kates (1965) and Soulsby (1965a).

As all the parasites encountered in this study have a direct life-cycle, the development and survival of the free-living stages are vitally affected by weather and climate. Levine (1963) as defined weather as: "a composite of atmospheric conditions—temperature, barometric pressure, precipitation, humidity, wind direction and velocity, sunlight, and so forth, at a particular time. Climate is a sum of weather conditions over a longer period of time." The climate at Outeniqua is temperate, with a mild winter, generally moist at all seasons, with a warm summer.

Gordon (1958) stated: " The basic ecological concept is that almost every animal in the flock is infested, and that the environment is contaminated continuously". This was confirmed in a previous study at Outeniqua, when it was shown that worm egg counts reached maximum peaks in winter and spring, the greatest contamination occurring in spring (Muller, 1964).

Gordon (1958) postulated that the free-living stages of each species developed best under different conditions of temperature and moisture.

Muller (1964) was unable to draw any conclusions as to the ultimate fate of the eggs or of the hatched larvae, but the problem was solved in the first experiment of the present study by the exposure of worm-free lambs to infested pasture for the limited period of 28 days. This method had three distinct advantages:—

(i) The normal grazing habits of the specific host ensured the acquisition of available infective larvae;

(ii) The use of the specific host to test the viability of the infective larvae;

(iii) Removal of the host, before any possible host-parasite reaction could take place.

It is freely admitted that the third advantage is based on empirical grounds as the rapidity of reaction by the lamb to infestation with any species is as yet not fully known.

Spring-summer infestation

For the purpose of this discussion, this will be regarded as that period extending from October to March. It will be noted that *heavy* infestations were recorded in October 1960, following the well distributed rains in September. From November onwards, the degree of pasture infestation fell off rapidly to reach its lowest level in December, rising gradually to the end of February, and, thereafter, increasing markedly in March (Fig. 1, Appendix Table 2).

The relatively small numbers of parasites recovered in November are in direct contrast to the extremely high counts recorded in March. During both of these months the mean maximum (25° C) and the mean minimum (15° C) were identical. A possible explanation for the low levels of infestation, which were recorded in November, is the design of the experiment where two lambs were exposed to infestation for a period of two weeks only (the third lamb being exposed for four weeks). The extremely dry October (3·0 mm) would also affect the availability of infective larvae.

By contrast, considerably more rain fell in February (73·2 mm) and, furthermore, the " Indicator " lambs were left on the pasture for four weeks, thus materially influencing the number of infective larvae ingested.

The worm burdens of Groups B and C declined during the period October to December (Fig. 3 and 5). In the latter group the decline was in all probability the result of a " self-cure ", while the number of adult worms in Group B was naturally low. Muller (1964) has shown that worm egg counts during this particular period in the years 1959–1961 were at a low level. The direct consequence was decreased contamination of the pastures, i.e. a lowered " biotic potential ". Despite the favourable climatic conditions, high temperatures and adequate rainfall, the infective phase of " biotic realization " was not enhanced (Dinaberg, 1944a, b; Gordon, 1948; Dinnik & Dinnik, 1958).

As stated by Levine (1963) temperature and precipitation are not the only factors affecting the availability of infective larvae. Other factors, such as the evapotranspiration (evaporation of soil moisture plus transpiration of the plants), soil moisture supply and plant cover cannot be ignored, and must of necessity influence the survival rate of the free-living stages. The estimation of these factors was beyond the scope of these experiments and thus could not be critically assessed.

It would appear that at Outeniqua there is a negative correlation between the availability of infective larvae and the mean monthly mean temperatures. During the period mid-November to mid-March, when the mean temperature is 20° C or higher, there is a notable depression in the numbers of larvae available on the pastures (Appendix Table 2). Conversely, pastures were heavily infested at those times when the mean temperature varied between 14° and 17° C (see below—Autumn-winter Infestation).

Parnell (1962) conducted a survey on the seasonal variations in worm burdens in young sheep in South Western Australia, and observed that most infective larvae died off rapidly after the middle of spring as the result of desiccation and sunlight. At Outeniqua, temperatures in summer are high and the sunlight intense, with no trees to provide shade. During the heat of the day the sheep stand in groups with their heads down, seeking the shade provided by one another's bodies. At certain times the atmosphere becomes extremely hot and arid, with severe desiccation, as the result of a phenomenon known as " berg winds ". These are usually north or north-easterly winds, which, blowing over the Outeniqua mountains, and swooping down on the plains below, become heated as the result of compression from the high to the low altitude. The heat and desiccation caused by these " berg winds " are not reflected by the conventional recordings in the Stevenson screens. These factors can and do affect the viability of the free-living stages. Kates (1965) in his review on ecology stated that " larval stages of nematodes exposed to direct sunlight during warm seasons may be killed by the heat generated in or on the soil, by the drying effects of intense sunlight, by the injurious effects of ultra violet light or by all three factors combined ". Moreover, Kates contended that the combined effect of sunlight and desiccation could render the soil helminthologically sterile.

The low " biotic realization " is reflected in the worm recoveries of Group A where the average total nematode burdens of sheep killed in December were 1,608 and 320; in January, 1,308 and 1,179. These recoveries were the lowest recorded during the whole of the experimental period, and confirm the unfavourable ecological conditions for the free-living stages.

The prevailing climatic conditions during the summer are extremely favourable for *H. contortus*, according to the generally accepted standards (Dinaberg, 1944a, b; Gordon, 1948, 1950, 1953; Kates, 1950; Dinnik & Dinnik, 1958; Levine, 1959, 1963; Silverman & Campbell, 1959; Crofton, 1963; Soulsby, 1965a). These favourable conditions were reflected by the relative increase in *H. contortus* in January, which, however, were not maintained.

Egg counts were falling from October to January (Muller, 1964), and the general failure of the " biotic realization " of the already reduced number of eggs deposited on the pasture, can be explained by—

(i) rapid hatching and development of pre-infective stages;

(ii) high mortality of these pre-infective stages as the result of the depletion of energy reserves, associated with high temperatures;

(iii) other unknown factors detrimental to the survival of nematode larvae, despite adequate, well distributed rains in November, December and January. Similar observations on the reasons for the failure of the " biotic realization " have been made by Kates (1965).

During December and January *Trichostrongylus* spp. were the least numerous of the three major genera, while in January *H. contortus* was the most numerous. In February the genera occurred in the following numerical order: *Trichostrongylus* spp., *Ostertagia* spp. and *H. contortus*. By February, the numbers of adult worms of all species in Groups B and C had increased considerably. More eggs were passed in the faeces, and the " biotic potential " markedly increased. With a mean monthly mean temperature of 20·3° C and well distributed, adequate rains, the climate in March favoured the " biotic realization " (Appendix Table 1). This is substantiated by the fact that worm burdens had increased by four- to sevenfold in that month (Appendix Table 2 and Fig. 1).

Autumn-winter infestation

There was an ever-increasing degree of infestation of the pastures from autumn to the end of winter (April to September 1961). The mean monthly maximum temperatures for this period varied from 19·2° to 23·1° C; the mean monthly minimum from 9·3° to 14·5° C, and the mean monthly mean from 14·6° to 18·2° C. With the exception of June 1961, when 6·1 mm was recorded on one day only, the rainfall, varying from 38·6 mm to 71·9 mm per month, was well distributed (Appendix Table 1).

The lack of moisture in June was partly responsible for the drop in the degree of pasture infestation, as is shown by those " Indicator " lambs, grazing from 7 June to 6 July, and from 21 June to 20 July. They had average worm burdens of only 266 and 1,717, respectively (Appendix Table 2). The drafting of the sheep to the new pastures further decreased the infestation which was, however, only of short duration.

Crofton (1952) found low concentrations of infective larvae on newly seeded pastures despite the high stocking rate when such pastures are utilized for the first time. Crofton (cited by Soulsby, 1965a) contended that, although the degree of pasture infestation may tend to be greater on reseeded pastures because of the higher stocking rate, the lack of a protective " mat " of old and decaying plant material would tend to reduce the longevity of the larvae, and thus the available viable larval population, despite the greater degree of pasture contamination. Crofton's postulates are not substantiated at Outeniqua, where the nature of the new pastures in July, i.e. tall, dense growth of lupins (1·0 to 1·5 metres) and dense, lush growth of oats, but lacking a " mat ", plus the very favourable climatic conditions, resulted in a massive build-up of infestation within six weeks.

This massive infestation is illustrated by the recoveries from the " Indicator " lambs slaughtered on 3 and 16 August, after exposure for four weeks on these new pastures. Average worm counts in these two groups were 7,924 and 11,262, respectively. The results prove categorically that optimal conditions for the free-living stages of all genera applied during this brief period.

This build-up occurred in July and August, at a time when the mean monthly mean temperatures were 14·6° and 14·9° C, respectively, i.e. during the coldest months of the year (Appendix Table 1).

To recapitulate, three major factors contributed to this heavy winter infestation at Outeniqua:

(i) Intensive contamination of the pastures, particularly by the heavily infested lambs (Group B), and to a lesser extent, by the yearlings and adults (Group C);

(ii) Adequate moisture as the result of well distributed rains;

(iii) Relatively low temperatures, resulting in lowered mortality of the free-living stages. Moisture, temperature and the type of pasture provided ideal conditions for the " biotic realization ".

Ecology of individual genera

The most numerous parasites at Outeniqua were *Trichostrongylus* spp., except for a limited period during summer. As soon as the mean temperatures dropped below 20° C in early autumn, however, recoveries increased rapidly. The observation that the free-living stages of this genus thrive in cool moist conditions, is confirmed by the observations of other workers (Mönnig, 1930; Hawkins, Cole & Kline, 1944; Kates, 1950; Silverman & Campbell, 1959; Levine, 1963; Crofton, 1963).

The temperature and moisture requirements of *Ostertagia* spp. are similar to those of *Trichostrongylus* spp., since the greatest numbers were recovered during the cooler, moist months, from autumn to spring (May to September). The warm summers, with the possibilities of high evaporation, are detrimental to the free-living stages of both species. This confirms the observations of Rogers (1940), Kates (1950), Gordon (1953, 1958) and Levine (1963).

Although both *Trichostrongylus* spp. *and Ostertagia* spp. were numerically dominant in the winter, there were concomitant heavy infestations of *H. contortus*, *Cooperia* spp., *Nematodirus* spp. and, to a lesser extent, of *O. venulosum* and *C. ovina*.

The relatively small numbers of infective larvae recorded during the summer at Outeniqua are in all probability the result of light pasture contamination (Muller, 1964) combined with the deleterious effects of intense sunlight, heat and evaporation on the free-living stages (Kates, 1965).

The free-living stages are important phases of the biology of the parasites, and the degree of availability of viable infective larvae on the pasture is shown by the " Indicator " lambs (Group A). The degree of infestation of the grazing flock, which is continually contaminating the pasture and simultaneously becoming infested, is governed by the availability of infective larvae. An examination of the data of recoveries from the three groups, confirms these statements. In all three groups the sheep showed that the highest incidence of all genera was from autumn through the winter to spring (mid-March to mid-September). With the exception of *H. contortus* which showed a relatively minor increase during January and February, there was pronounced depression of the major species in summer.

Similar observations on the ecology of the free-living stages were made by workers in Scotland (Morgan *et al.*, 1951; Parnell *et al.*, 1954), in England (Crofton, 1954), in the winter rainfall regions of Australia (Gordon, 1953, 1958; Forsyth, 1953; Parnell, 1962) and in New Zealand (Brunsden, 1963; Tetley & Langford, 1965).

Numerous workers have stated that optimal conditions for the development of infective larvae vary, and that individual genera developed at different times of the year (Tetley, 1941; Gordon, 1953, 1958; Crofton, 1954, 1963; Baxter, 1957; Gibson, 1958; Thomas, 1959; Durie, 1962; Parnell, 1962; Brunsden, 1963; Reinecke, 1964; Barrow, 1964; Rossiter, 1964; Viljoen, 1964). These observations were not confirmed by the results at Outeniqua which show that all parasites find conditions optimal for the development, and survival, of their free-living stages during autumn, winter and early spring.

(ii) *Parasitic stages in the specific host*

It is axiomatic that every animal is infested to a greater or lesser degree. The factors which determine the degree of infestation at any given point of time are extremely complex. Factors which affect the degree of parasitism are *int. al.* the availability of the infective larvae on the pastures; the physiology and the nutritional status of the host, which, in turn, affects the susceptibility of the host to infestation; and, finally, the interaction between the host and the parasite.

Larval stages in the specific host

There was a high incidence of worms retarded in their development, particularly in the winter months. In *Trichostrongylus* spp. the proportions of fifth stage or adolescent worms increased, and the numbers of fourth stage larvae of *H. contortus*, *Ostertagia* spp., and to a lesser extent, *Nematodirus* spp. increased at the expense of the adults.

Many workers have recorded the fact that the fourth stage larvae of various genera are found in large numbers during the winter and early spring (Morgan *et al.*, 1951; Somerville, 1954; Field, Brambell & Campbell, 1960; Parnell, 1962; Michel, 1963; Dunsmore, 1963; Rossiter, 1964; Viljoen, 1964; Anderson, Armour, Jennings, Ritchie & Urquhart, 1965; Soulsby, 1965b).

Morgan *et al.* (1951) and Parnell *et al.* (1954) found that fourth stage larvae of *Ostertagia* spp. and *H. contortus* regularly accumulated in sheep slaughtered in January in Scotland. These workers attributed this accumulation to newly acquired larvae. The climatic conditions prevailing at that time (January), however, preclude the survival of sufficient numbers of free-living infective larvae, since, to quote these authors, " the pasture was still mainly covered with snow, and only a few windswept patches were available for grazing ".

In South Africa, both Rossiter (1964) and Viljoen (1964) recorded large numbers of fourth stage larvae of *H. contortus*, *Ostertagia* spp. and *Oesophagostomum columbianum* (Curtice, 1890) over the winter months. These authors suggested that these accumulations could be the result of the immune reaction on the part of the host.

A hypothesis for the larval accumulation in the host

The accumulation of fourth stage larvae of most genera, and in the case of *Trichostrongylus* spp., the fifth stage or immature adults, over the winter months in the host, is a normal phenomenon or stage in the life-cycle of the nematode parasites of the sheep. This is substantiated by the following facts:—

(i) Fourth stage larvae of *H. contortus* show a definite preponderance over adults in all groups, including Group A (" Indicator " lambs).

(ii) The ratio of fourth stage larvae to adults of *Ostertagia* spp. shows a marked increase.

(iii) The numbers of adolescent stages, i.e. immature adults of *Trichostrongylus* spp. when compared with those of sexually mature adults, show similar increases, particularly in Group B.

This accumulation of retarded forms is not the result of a reaction by the host on the parasites, because this phenomenon is also recorded in the "Indicator" lambs (Group A). Moreover, it occurs in all groups in the winter months, and is thus obviously seasonal.

The fourth stage larvae of *Nematodirus* spp. repeat the phenomenon of the winter accumulation in a fashion similar to *Ostertagia* spp. in Group A. The dominance of fourth stage larvae in Groups B and C could be the result of an immune reaction, although the marked increase in larval recoveries during the cool months of 1960 and 1961, is no doubt an example of the overwintering phenomenon (see Fig. 8).

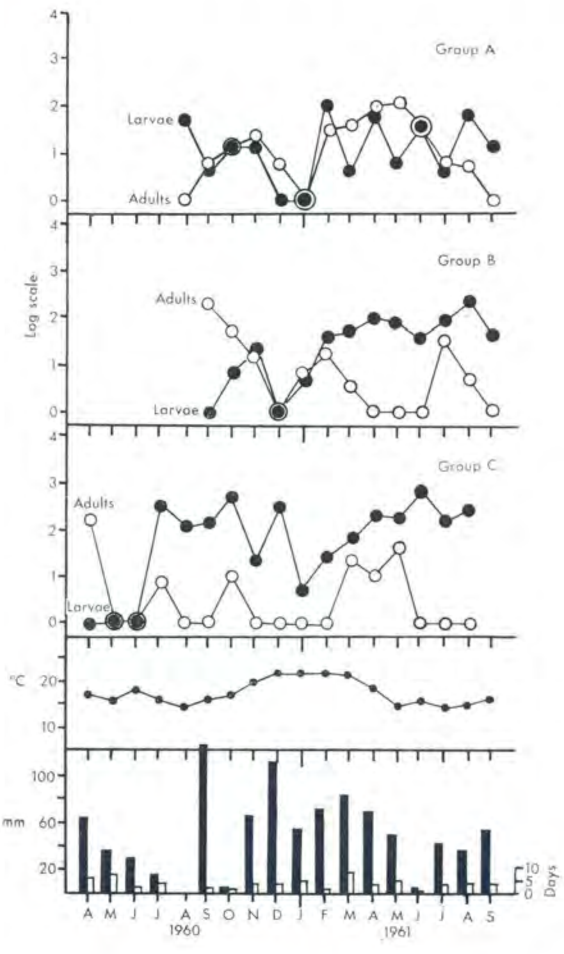

FIG. 8.—Incidence of adults and larvae of *Nematodirus* spp. in Groups A, B and C

Although the recoveries of fourth stage larvae of *Cooperia* spp. were not as numerous as those of the preceding genera, there was a tendency to a winter accumulation, particularly in Groups A and B.

It is obvious that the annual exposure of the free-living stages of the parasites to extremely adverse climatic conditions in winter varying from the snow and ice of the northern hemisphere, to either dry or wet conditions with severe frost in many parts of South Africa, would, sooner or later, have resulted in the almost complete elimination of the parasites. However, by overwintering in the gastro-intestinal tract of the host, the parasite has ensured itself of a remarkably stable environment, with ideal conditions of temperature, moisture and food.

The delay in the developmental cycle of the parasite is an expression of biological economy, ensuring the maturation of the retarded (overwintering) stages to sexually mature worms at a time when the contamination of the pastures (eggs to third stage) would be synchronized with the availability of susceptible hosts (lambs). The bionomics of the parasites are inextricably geared to those of their hosts, since the normal lambing time of sheep is in spring, at a time when the food supply for the hosts is increasing, and the whole biological system of nature is on the upsurge.

Crofton (1963) stated that the phenomenon of delayed development is common to all trichostrongyles of sheep.

The postulation of Dikmans & Andrews (1933) that *Ostertagia* spp. develop to the patent phase in the mucosa has subsequently been shown by Somerville (1954) not to be completely correct, as only some larvae are retarded in the histotrophic phase, and this was confirmed by other workers (Dunsmore, 1963; Michel, 1963; Soulsby, 1965b). Anderson, Armour, Jennings, Ritchie & Urquhart (1965) working with *O. ostertagi* in calves, found evidence that the histotrophic phase of the fourth stage larvae was a phenomenon of overwintering.

The dramatic fall in worm burdens of *Ostertagia* spp. in July in the " Indicator " lambs, is not reflected in the worm counts of Group B, which showed increasing numbers of both larvae and adults. In other countries, where there is a decrease in the intake of infective larvae, the overwintering larvae in the histotrophic phase start maturing to adults to replace those dying from various causes (Michel, 1963; Dineen, 1963; Dunsmore, 1963, 1965). Large numbers of " inhibited " fourth stage larvae of *Nematodirus* spp. were recorded in Groups B and C. Donald, Dineen, Turner & Wagland (1964) in assessing the dynamics of the host-parasite relationship, similarly found large numbers of retarded fourth stage larvae of *N. spathiger*, and concluded that these retarded larvae were an expression of the immunological control by the host. This is seen particularly in Group C, and could be assumed to confirm the postulates of Donald *et al.* (1964).

There was a greater accumulation of larvae of *Nematodirus* spp in Groups A and B in winter than in the other seasons. This substantiates the contention that this genus also overwinters in the host.

The contention of Field *et al.* (1960) that the maturation of the latent larvae within the host played a vital role in the phenomenon of the " spring rise " of faecal egg counts is further support for the theory that the over-wintering of larvae is a basic phase of the life-cycle.

Parnell (1962) also suggested that the retarded larvae, especially in the histotrophic phase, were the cause of the " summer rise " in weaners, as well as being the cause of the " parturient rise " in lambing ewes.

Both Viljoen (1964) and Rossiter (1964) reported higher burdens of fourth stage larvae of *H. contortus* and of *O. columbianum* and, to a lesser extent, of *Ostertagia* spp. during the winter period.

Reinecke (1964) confirms the contention that the larvae of the major genera of the summer rainfall areas, *H. contortus*, *O. columbianum* and, to a lesser extent, *Ostertagia* spp., overwinter in sheep. His postulation that the retardation of the larvae is an expression of host resistance cannot be supported. The author has found further confirmation for his hypothesis in the results published by Anderson, Armour, Jennings, Ritchie & Urquhart (1965) working with calves to determine the availability of *Ostertagia ostertagi* larvae. They reported that low numbers of inhibited fourth stage larvae were present during the European summer; whereas with the approach of winter, the proportions of inhibited fourth stage larvae of both *O. ostertagi* and *Cooperia oncophora* increased considerably. Anderson, Armour, Jarrett, Jennings, Ritchie & Urquhart (1965) stated that the inhibition of both *Ostertagia* spp. and *Cooperia* spp. was recorded from late October onwards, and that complete inhibition of development occurred in worm-free calves, which had grazed for only 14 days.

It could be argued that, since worm burdens increased in winter, due to a greater intake of infective larvae, overcrowding could result in inhibition of development or growth. The fact that the phenomenon of overwintering of fourth stage larvae, particularly of *H. contortus* and *Ostertagia* spp. was recorded in the " Indicator " lambs (Group A), even during that period in July, when the numbers of available infective larvae decreased dramatically, refutes the argument of over-crowding.

The adult stages in the specific host

The incidence of the various species of the genus *Trichostrongylus* varied with age. While the lambs (Group B) were under the age of nine months, both *T. colubriformis* and *T. falculatus* were dominant. When the animals were 18 months or older, *T. axei* was recorded in ever-increasing numbers (Fig. 7, Appendix Tables 3 and 4). In the adult sheep (Group C) relatively low numbers of *T. colubriformis* and *T. vitrinus* were recovered, confirming the observations of Tetley (1949) that adult sheep are not prone to infestation by these species.

Significant numbers of adult *T. axei* were recovered during the artificial digestion of the abomasal wall. The possibility that *T. axei* undergoes a histotrophic phase in its life-cycle, particularly in adult sheep, cannot be excluded. The postulation of Parnell (1962) that this species undergoes a histotrophic phase, is confirmed by these observations.

Roberts (1951) found *Cooperia* spp. to be plentiful in calves up to the age of 12 to 16 weeks, but rare in older animals. In the present experiments, relatively few recoveries of *Cooperia* spp. were recorded in lambs under 12 months of age (Group B). By comparison, in the older animals (18 to 24 months) in Group C, large numbers of this genus were recorded. It appears that *Cooperia* spp. are parasites of older animals rather than of lambs.

Reactions between species

Because of the large variety of parasites at Outeniqua, it would be reasonable to assume that reactions between genera, and also between species within a genus, could take place.

Experimental evidence of inter-generic reactions has been recorded by various authors (Turner & Colglazier, 1954; Shumard, Bolin & Eveleth, 1957; Turner, Kates & Wilson, 1962; Durie, 1962; Reinecke, 1966).

Turner & Colglazier (1954), working on lambs with mixed infestation of *H. contortus* and *N. spathiger*, found that infestations with *H. contortus* usually reversed the self-limiting course of *N. spathiger*. The percentages of immature parasites recorded by these authors approximate those recorded in Groups B and C (Appendix Tables 3 and 4).

Shumard *et al.* (1957) experimentally infested lambs with *H. contortus*, *T. colubriformis* and *N. spathiger* and showed that when there is a preponderance of *T. colubriformis* the burdens of *H. contortus* and *N. spathiger* are always low. This is confirmed in Group B (Appendix Table 3). In Group C, *T. colubriformis* was not numerically dominant and this interaction was not confirmed (Appendix Table 4).

Turner *et al.* (1962) and Durie (1962) found that in simultaneous infestations of *H. contortus*, *O. circumcincta* and *T. axei*, there was evidence of depression of the former two species by the latter. At Outeniqua it was observed that where *T. axei* was predominant (Group C) the depression of *H. contortus* was notable, while the numbers of *O. circumcincta* were affected to a lesser extent (Appendix Table 4).

Reinecke (1966) attempted to infest worm-free lambs experimentally with mixed infestations of *int. al. O. circumcincta*, *H. contortus* and *T. colubriformis*. He found that the establishment of uniform burdens of *H. contortus* was adversely affected by the presence of *O. circumcincta*, and that the interaction between these two parasites could take place within 32 days of infestation.

At Outeniqua, climatic conditions during the summer months of 1960–61 were extremely favourable for the free-living stages of *H. contortus* which actually were the dominant infestation on the pasture in January (Group A, Fig. 2, Appendix Table 2). This should have resulted in a classic outbreak of haemonchosis in Group B and even in the older sheep of Group C. Recoveries of *Ostertagia* spp., however, were numerically dominant in December and January, while it was only in February that *H. contortus* was dominant. The increased assimilation of infective third stage larvae of both *Ostertagia* spp. and *T. axei* in March, most probably further suppressed the *H. contortus* infestation, and resulted in the subsequent "self-cure" of *H. contortus* (Stewart, 1950, 1955).

In the previous discussion on the ecology of the free-living stages in the summer months, no explanation was given for the fact that the infective stages of *H. contortus*, while present on the pasture in considerable numbers, did not result in anything more than a moderate infestation of the grazing animals. The author contends that the dominance of *Ostertagia* spp., and in older sheep, of *T. axei* particularly, was the reason for this phenomenon.

SUMMARY

1. The epizootiology of nematode parasites of sheep was investigated at the Outeniqua Experimental Farm, George, Cape Province.

2. There was a negative correlation between temperature and the availability of infective larvae on the pasture. During spring and summer when the mean average mean temperatures exceeded 20° C, low recoveries were recorded; whereas maximum recoveries were made when the mean temperature varied between 14° and 17° C in autumn and winter.

3. The major parasites at Outeniqua were *Trichostrongylus* spp., *Ostertagia* spp. and to a lesser degree *H. contortus*, *Cooperia* spp. and *Nematodirus* spp.

4. Flocks acquired massive worm burdens during the cooler months of the year, from autumn to spring.

5. The massive build-up of retarded fourth stage larvae and immature adults is a physiological process in the life-cycle, whereby the parasite ensures itself of optimal circumstances for survival against adverse climatic conditions.

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TABLE 1.—*Climatic data at Outeniqua from April* 1960 *to October* 1961

Month	Rainfall		Temperature		
	Total	No. of days rain fell	Mean maximum	Mean minimum	Mean monthly mean
	mm		°C	°C	°C
April 1960	63·5	7	21·5	11·9	16·7
May	38·1	8	21·1	10·2	15·6
June	29·2	3	25·9	10·3	18·1
July	8·4	4	23·8	8·9	16·3
August	0·0	0	19·4	9·6	14·5
September	121·4	3	21·2	11·0	16·1
October	3·0	1	22·9	12·3	17·6
November	66·5	4	24·8	15·0	19·9
December	113·0	5	26·3	16·4	21·3
January 1961	55·6	6	26·6	16·9	21·7
February	73·2	2	27·1	16·2	21·6
March	85·6	10	25·0	15·7	20·3
April	71·9	4	21·9	14·5	18·2
May	51·3	6	19·2	10·6	14·9
June	6·1	1	20·3	11·0	15·6
July	41·7	4	19·6	9·7	14·6
August	38·6	6	20·5	9·3	14·9
September	56·1	5	23·1	9·9	16·5
October	64·2	9	23·2	9·5	16·3

Table 2 Group A "Indicator" lambs. Worms recovered at autopsy T

Sheep No.	Date of birth	Date to pasture	Date killed	*Trichostrongylus* spp. Fourth stage larvae	*T. colubriformis*	*T. falculatus*	*T. axei*	*T. pietersei*
004	1960—20 May	1960— 3 Aug.	1960—17 Aug.	0	0	0	0	0
K 603	14 May	3 Aug.	17 Aug.	0	0	0	0	0
003	20 May	3 Aug.	31 Aug.	2,825	0	800	1,455	0
K 605	28 June	17 Aug.	31 Aug.	450	0	0	640	0
603	20 May	17 Aug.	31 Aug.	190	750	0	334	0
005	29 June	17 Aug.	14 Sept.	0	500	0	80	0
K 609	30 June	31 Aug.	14 Sept.	60	0	0	0	0
608	30 June	31 Aug.	14 Sept.	0	0	0	0	0
008	1 July	31 Aug.	28 Sept.	965	300	0	400	0
6010	3 July	14 Sept.	28 Sept.	756	412	0	0	0
K 6014	3 July	14 Sept.	28 Sept.	975	0	0	166	0
K 6016	3 July	14 Sept.	12 Oct.	1,421	0	57	0	0
6011	4 July	28 Sept.	12 Oct.	123	525	0	412	0
0015	5 July	28 Sept.	12 Oct.	182	43	0	0	0
0016	5 July	28 Sept.	26 Oct.	222	0	0	189	0
0017	5 July	12 Oct.	26 Oct.	1,589	0	392	134	0
K 6018	5 July	12 Oct.	26 Oct.	411	380	766	128	70
K 6019	5 July	12 Oct.	9 Nov.	572	494	655	101	21
6012	6 July	26 Oct.	23 Nov.	0	3	0	0	0
K 6020	5 July	26 Oct.	23 Nov.	184	500	453	0	124
0018	6 July	26 Oct.	23 Nov.	0	8	0	0	0
K 6021	6 July	9 Nov.	7 Dec.	0	0	0	0	0
K 6022	6 July	9 Nov.	7 Dec.	0	106	425	0	106
K 6023	9 July	23 Nov.	7 Dec.	483	0	0	0	0
K 6025	7 July	23 Nov.	21 Dec.	0	31	55	0	0
K 6026	7 July	7 Dec.	1961— 4 Jan.	Discarded		—	—	—
K 6027	7 July	7 Dec.	4 Jan.	0	320	0	0	0
6013	8 July	7 Dec.	4 Jan.	0	3	0	0	0
K 6028	8 July	21 Dec.	18 Jan.	0	80	27	0	0
K 6029	8 July	21 Dec.	18 Jan.	216	16	53	0	0
K 6030	8 July	1961— 4 Jan.	1 Feb.	234	425	0	0	0
K 6031	8 July	4 Jan.	1 Feb.	150	413	511	0	0
6014	10 July	18 Jan.	15 Feb.	140	35	12	0	0
6015	10 July	18 Jan.	15 Feb.	226	393	0	0	0
0019	10 July	1 Feb.	1 March	1,550	7	45	0	0
K 6032	10 July	1 Feb.	1 March	330	65	0	0	0
K 6033	10 July	15 Feb.	15 March	5	595	1,588	0	0
K 6034	10 July	15 Feb.	15 March	Discarded		—	—	—
6016	11 July	1 March	28 March	781	2,186	2,187	0	33
0020	11 July	1 March	28 March	296	1,774	1,138	70	70
K 6035	11 July	15 March	12 April	247	4,758	3,405	32	168
K 6036	11 July	15 March	12 April	168	2,329	2,828	0	88
6017	12 July	29 March	26 April	284	684	1,128	40	250
K 6037	12 July	29 March	26 April	305	2,744	1,087	42	66
K 6038	13 July	12 April	9 May	81	0	30	0	0
6022	15 July	12 April	9 May	199	1,201	919	390	84
6023	15 July	26 April	24 May	568	6,438	1,843	97	948
0031	20 July	26 April	24 May	137	5,302	4,368	0	93
0036	17 Aug.	9 May	7 June	484	1,345	202	0	101
0037	17 Aug.	9 May	7 June	458	7,473	5,200	1,250	410
0038	20 Aug.	23 May	22 June	580	880	367	87	147
0042	24 Aug.	23 May	22 June	156	1,013	27	120	26
0046	26 Aug.	7 June	6 July	20	0	0	0	0
0047	26 Aug.	7 June	6 Ju.y	50	30	0	0	30
0048	26 Aug.	21 June	20 July	367	331	83	0	0
0052	28 Aug.	21 June	20 July	157	175	76	20	0
0054	28 Aug.	5 July	3 Aug.	875	948	507	0	204
0055	29 Aug.	5 July	3 Aug.	770	1,211	0	204	101
0059	31 Aug.	19 July	16 Aug.	2,449	1,634	306	0	408
0062	5 Sept.	19 July	16 Aug.	213	524	0	51	22
0063	5 Sept.	2 Aug.	31 Aug.	2,139	268	82	123	11
E 015	5 Sept.	2 Aug.	31 Aug.	5,157	3,635	489	62	1,616
K 619	1961—22 May	14 Aug.	13 Sept.	256	1,740	120	0	900
6130	22 May	14 Aug.	13 Sept.	1,340	3,209	200	0	1,317
6110	22 May	14 Aug.	13 Sept.	668	1,747	57	0	288

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TABLE 2.—*Group A " Indicator " lambs. Worms recovered at autopsy* (cont.)

T. vitrinus	*Ostertagia* spp. Fourth stage larvae	*O. circumcincta*	*O. trifurcata*	*O. ostertagi*	*Haemonchus* sp. Forth stage larvae	*H. contortus*	*Cooperia* spp. Fourth stage larvae	*C. curticei*	*C. punctata*	*C. pectinata*	*C. spatulata*
0	0	0	0	0	0	0	67	0	0	0	0
0	0	0	0	0	83	0	0	0	0	0	0
1,062	2,185	475	20	0	0	0	0	0	0	0	0
900	40	900	0	0	0	0	0	0	0	0	0
0	20	728	0	0	0	0	0	0	0	0	0
0	330	193	0	0	0	22	0	0	0	0	0
0	0	750	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	221	821	0	0	0	0	0	0	0	0	0
0	848	161	0	0	0	0	0	0	0	0	0
0	400	166	0	0	160	0	0	0	0	0	0
0	3,336	5,034	179	0	599	512	0	0	0	0	0
203	635	297	63	0	720	187	0	0	248	0	0
0	218	637	0	0	0	0	0	0	0	0	0
0	208	1,078	0	0	143	0	0	0	0	0	0
0	2,080	464	66	0	2,238	77	46	83	0	0	0
169	415	759	0	0	1,381	52	78	58	0	0	0
85	1,200	2,245	506	102	568	1,077	47	178	51	0	0
0	0	82	18	0	0	489	0	0	0	0	0
41	161	1,361	479	0	25	283	0	165	0	0	0
0	0	107	11	0	0	439	0	8	0	0	0
0	176	178	59	0	35	350	0	0	0	0	0
0	25	287	143	0	25	416	0	89	0	0	0
0	1,633	0	0	0	161	0	0	0	0	0	0
0	0	73	35	0	0	103	0	9	3	0	0
—	—	—	—	—	—	—	—	—	—	—	—
0	0	6	3	3	0	117	0	80	0	0	0
0	0	613	0	0	0	917	0	0	0	0	0
0	0	235	103	15	0	277	0	0	0	0	0
0	137	28	67	0	867	234	0	0	0	0	0
0	959	215	120	0	769	124	186	0	0	437	0
59	0	10	0	0	0	22	0	59	59	59	118
0	35	5	3	0	172	43	0	0	0	0	0
0	452	63	11	0	205	100	0	0	0	0	0
0	2,445	21	12	0	870	72	0	0	0	0	0
0	153	14	27	0	366	61	0	0	0	0	0
0	40	1,005	251	0	100	110	5	0	198	0	0
—	—	—	—	—	—	—	—	—	—	—	—
0	655	1,420	55	0	1,252	120	4	0	0	396	0
0	193	428	78	0	862	436	46	0	0	0	45
419	188	482	289	33	1,004	167	0	335	84	335	0
176	52	234	156	0	105	155	0	85	171	171	0
0	58	570	80	0	145	240	0	375	103	20	0
66	736	1,421	386	0	565	157	69	398	25	133	133
0	235	62	0	0	1,124	468	30	0	0	0	0
0	146	2,039	335	39	451	987	0	575	343	173	172
363	935	1,901	483	0	1,417	393	0	1,366	1,538	0	0
240	121	1,160	614	31	794	276	0	233	116	350	117
51	464	882	54	0	533	54	16	51	0	0	454
274	486	1,115	334	0	2,640	98	14	135	135	0	0
73	748	2,540	519	43	1,949	173	0	293	660	147	733
0	686	2,355	239	0	687	0	86	133	0	0	294
0	10	40	20	0	50	0	0	50	0	0	0
0	0	116	47	0	20	0	0	47	0	0	0
83	21	129	129	0	264	77	73	83	0	0	0
0	202	407	140	0	304	0	116	76	0	0	0
68	476	3,167	505	168	803	1,178	0	543	0	0	271
114	823	568	0	0	595	568	114	202	0	0	303
306	2,208	5,617	963	102	2,032	795	47	0	0	0	0
0	1,446	1,806	358	51	661	51	80	23	0	23	0
5	398	1,292	308	184	482	307	189	19	0	11	0
404	2,456	4,636	865	62	3,033	0	33	0	0	0	0
660	1,532	1,526	280	73	445	0	11	120	0	0	0
735	1,666	708	41	4	0	389	0	198	0	0	66
403	7,164	1,440	224	16	256	0	84	345	0	0	0

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Table 2. "Indicator" lambs. Worms recovered at autopsy. (cont.)

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Nematodirus spp. Fourth stage larvae	*N. spathiger*	*N. filicollis*	*Bunostomum* sp. Fourth stage larvae	*B. trigonocephalum*	*Oesophagostomum* sp. Fourth stage larvae	*O. venulosum*	*Chabertia* sp. Fourth stage larvae	*C. ovina*	*Trichuris globulosa*	*Trichuris parvispiculum*	*Strongyloides papillosus*
67	0	0	0	0	270	0	20	0	0	0	67
0	0	0	0	0	0	0	0	0	0	0	400
5	0	0	0	0	0	0	0	0	0	0	0
150	0	0	0	0	0	0	0	0	0	0	150
0	0	0	0	0	0	0	0	0	0	0	100
0	0	0	0	0	0	3	0	2	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
25	100	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	1
0	0	0	0	0	0	1	0	0	0	0	0
0	0	0	12	0	0	0	0	0	0	0	0
0	0	0	0	0	30	0	0	0	0	0	0
16	395	0	0	0	0	0	0	0	0	0	0
138	84	0	0	0	0	0	0	0	2	0	0
117	146	23	0	0	50	0	0	0	0	0	0
189	11	0	0	0	33	0	0	0	0	0	0
0	21	0	0	0	0	0	0	1	0	0	0
0	73	43	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	13	0	0	0	0	0
3	53	53	3	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	4	0	0	0
0	6	3	0	0	0	2	0	0	0	0	0
—	—	—	—	—	—	—	—	—	—	—	—
0	8	0	0	0	0	0	0	0	0	0	0
0	4	0	0	0	0	1	0	0	1	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	2	0	1	0
594	84	0	0	0	0	0	0	4	0	0	0
0	59	59	0	0	0	0	0	0	0	0	0
6	12	0	0	0	0	0	0	1	3	0	0
65	13	0	0	0	0	0	0	1	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	1	0	0	0
0	0	198	0	0	0	7	0	9	0	0	0
—	—	—	—	—	—	—	—	—	—	—	—
60	388	0	0	0	0	20	0	0	0	0	0
23	182	0	10	0	10	2	0	1	0	0	0
36	0	0	0	0	0	10	0	12	0	0	0
35	171	0	0	0	0	3	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
274	200	66	30	0	10	8	0	0	0	0	0
45	0	0	45	0	70	0	10	1	0	0	0
44	59	117	0	2	0	1	0	0	0	0	0
0	0	0	0	0	0	24	250	5	0	0	0
14	350	0	0	0	14	4	40	0	0	0	0
0	51	50	0	0	0	5	0	0	1	0	0
109	139	0	80	0	0	4	0	0	1	0	0
23	0	0	0	0	0	25	0	0	0	0	0
44	0	27	0	0	36	2	0	1	1	0	9
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	2	0	1	0	0	0
0	0	0	0	0	0	2	0	0	0	0	0
28	0	76	0	0	0	15	0	0	0	0	0
158	0	136	0	0	48	0	2	1	0	0	0
13	202	0	0	2	0	0	0	1	0	0	0
24	0	0	0	0	10	33	0	50	0	0	204
0	0	0	0	0	0	6	0	1	0	0	0
1,132	0	0	0	0	0	3	0	0	1	0	0
121	0	0	0	0	0	0	0	0	0	5	0
12	0	0	23	0	0	2	0	0	0	0	0
0	0	0	0	0	0	11	7	2	2	0	0
28	0	0	0	0	0	2	0	0	0	0	0

Table 3. Group B. lambs. Worms recovered at autopsy

Sheep No.	Date of birth	Date killed	*Trichostrongylus* spp. Fourth stage larvae	*T. colubriformis*	*T. falculatus*	*T. axei*
K 604	1960—28 June	1960—15 September	150	750	0	357
604	28 June	15 September	190	306	0	340
605	28 June	29 September	2,315	352	0	335
K 606	29 June	29 September	160	1,160	0	335
606	29 June	13 October	724	2,160	600	255
006	29 June	13 October	1,054	840	240	264
K 608	29 June	27 October	472	402	805	72
K 6010	30 June	27 October	123	25	20	16
0011	1 July	9 November	1,797	1,370	805	1,183
607	30 June	9 November	1,139	1,192	1,804	213
609	1 July	23 November	126	32	94	0
K 6011	1 July	23 November	37	121	0	25
K 6012	2 July	8 December	0	958	0	0
K 6013	2 July	8 December	0	19	9	0
0014	2 July	21 December	47	0	0	131
K 6015	3 July	21 December	Disc arded		—	—
K 6017	3 July	1961— 4 January	Disc arded		—	—
K 6018	13 July	4 January	0	8	0	24
6020	14 July	18 January	609	82	84	10
6019	14 July	18 January	630	33	0	0
6021	14 July	1 February	557	1,054	256	201
K 6039	14 July	1 February	123	5,528	5,295	759
K 6024	16 July	15 February	Disc arded		—	—
6026	16 July	15 February	1,842	666	31	4
K 6041	16 July	1 March	108	32	32	0
K 6042	16 July	1 March	319	60	198	0
K 6043	16 July	15 March	101	24	67	0
K 6044	16 July	15 March	123	3,654	4,609	22
K 6045	16 July	28 March	438	12,692	13,837	4,511
K 6046	16 July	28 March	316	6,299	8,822	223
0022	17 July	12 April	202	3,193	296	55
0021	17 July	12 April	530	802	493	0
6027	17 July	26 April	1,397	10,773	14,015	700
6028	17 July	26 April	1,550	10,912	8,794	1,284
0023	18 July	9 May	120	12,578	1,394	598
6029	17 July	9 May	207	11,404	2,748	218
0024	18 July	24 May	295	2,516	864	67
0025	18 July	24 May	512	2,306	882	411
0026	18 July	7 June	304	11,741	1,206	2,958
0027	18 July	7 June	550	82	400	20
0028	19 July	22 June	160	20,862	4,340	1,240
K 6047	19 July	22 June	237	3,592	231	1,489
0029	20 July	6 July	675	165	0	6,088
K 6048	19 July	6 July	61	700	0	856
0030	20 July	20 July	34	15,049	2,139	727
0032	21 July	20 July	720	110	0	1,384
6030A	26 July	3 August	497	15,215	2,977	2,530
6031	26 July	3 August	65	15,193	1,751	556
0033	1 August	16 August	1173	14,037	441	4,108
0034	3 August	16 August	354	7,547	1,437	1,437
6032	3 July	31 August	0	*4,013	1,050	1,788
6033	3 August	31 August	1,041	11,733	987	919

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* 148 *T. rugatus* were also present.

TABLE 3.—*Group B lambs. Worms recovered at autopsy* (cont.)

T. pietersei	*T. vitrinus*	*Ostertagia* spp. Fourth stage larvae	*O. circumcincta*	*O. trifurcata*	*O. ostertagi*	*Haemonchus* sp. Fourth stage larvae	*H. contortus*	*Cooperia* spp. Fourth stage larvae	*C. curticei*	*C. punctata*	*C. pectinata*	*C. spatulata*
0	0	0	104	70	0	0	187	0	0	0	0	0
0	0	210	143	0	0	0	0	0	340	0	0	0
0	0	312	685	0	0	300	28	160	0	0	0	0
0	0	335	1,210	0	0	300	161	210	0	0	0	0
0	92	618	1,026	114	0	600	0	20	180	0	0	0
0	0	252	736	0	0	0	172	10	122	0	0	0
315	47	591	18	0	0	0	81	19	0	26	0	0
3	0	551	80	17	0	42	0	0	6	0	0	0
372	412	1,707	1,043	358	0	0	0	0	29	31	0	10
40	252	1,848	1,736	153	33	962	830	0	27	27	0	26
0	0	0	313	23	0	0	812	0	0	0	0	0
0	96	275	227	16	0	38	303	0	0	0	0	0
0	0	0	1,640	544	0	0	0	0	0	0	0	0
0	0	0	34	4	0	0	0	0	0	0	0	0
0	7	93	861	233	0	0	7	0	0	0	0	0
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
0	0	0	620	426	0	0	205	0	0	0	0	0
0	19	300	117	25	0	105	30	30	0	7	0	0
0	0	534	99	28	0	132	54	0	0	0	0	0
70	149	314	694	270	0	0	446	21	0	0	0	0
0	216	28	1,328	50	0	84	1,014	0	0	0	0	0
—	—	—	—	—	—	—	—	—	—	—	—	—
0	6	1,540	138	76	0	1,860	137	0	0	0	0	0
0	0	84	21	0	0	873	291	0	0	0	0	0
0	0	189	33	22	0	210	384	0	0	0	0	0
0	33	593	107	34	5	413	270	0	0	0	0	0
3	904	1,209	878	293	0	13	19	15	328	0	0	0
558	1,117	1,158	5,903	1,092	164	384	328	0	0	0	0	0
834	682	463	2,756	449	0	471	589	0	0	0	0	0
2,743	57	906	855	168	28	1,931	131	0	0	0	0	0
123	0	357	993	62	0	922	588	0	0	0	0	0
1,597	392	1,341	3,204	609	0	3,290	1,654	267	0	0	0	0
423	1,271	1,706	1,989	546	90	2,303	544	49	0	0	0	0
238	335	369	234	0	0	612	0	0	0	0	0	0
1,554	2,959	2,751	2,779	652	0	3,304	245	0	0	187	0	186
288	96	5,417	1,151	372	0	1,768	0	16	0	940	0	0
104	20	829	1,918	483	96	1,094	46	0	0	103	0	0
1,033	1,378	1,702	970	0	0	4,170	47	0	0	0	0	0
123	0	450	123	62	0	766	246	78	320	400	160	80
3,464	2,154	300	800	240	0	780	40	0	0	0	0	0
349	232	229	4,573	986	0	2,148	1,805	0	0	0	0	0
0	0	2,996	2,426	696	0	10,153	881	9	4,765	0	0	669
0	0	427	2,832	499	0	2,012	398	0	0	0	0	0
1,339	631	477	10,258	721	52	6,373	0	100	0	0	0	0
419	0	182	3,002	73	0	1,250	0	32	0	0	0	352
8,592	861	2,288	3,068	455	0	7,920	1,363	43	4	0	0	0
2,880	1,148	245	51	101	0	1,176	0	0	0	0	0	0
3,174	1,103	1,120	2,187	426	68	4,770	0	13	441	0	0	220
1,294	442	708	4,273	390	0	4,767	1,156	10	442	0	0	166
6,094	148	910	10,160	3,934	536	8,785	1,609	0	0	0	0	0
7,817	2,221	2,705	657	84	0	6,450	291	186	246	0	0	0

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Table 3. Group B lambs. Worms recovered at autopsy (cont.)

Nematodirus spp. Fourth stage larvae	*N. spathiger*	*N. filicollis*	*Bunostomum* sp. Fourth stage larvae	*B. trigonocephalum*	*Oesophagostomum* sp. Fourth stage larvae	*O. venulosum*	*Chabertia* sp. Fourth stage larvae	*C. ovina*	*Trichuris globulosa*	*Trichuris parvispiculum*	*Strongyloides papillosus*
0	0	450	0	3	0	5	0	3	0	2	0
0	0	170	0	3	0	29	0	4	0	0	17
0	1	0	0	10	0	40	0	11	0	0	0
0	300	0	0	3	0	1	0	3	0	0	0
20	80	0	20	0	0	11	8	41	0	0	0
0	20	0	0	20	0	46	0	23	0	0	100
78	27	26	0	30	0	20	0	1	0	0	18
4	58	4	0	0	0	5	19	6	0	0	0
349	21	0	0	12	37	49	0	10	0	0	0
488	238	165	0	3	0	10	0	24	0	0	211
0	0	0	0	4	0	0	0	91	0	0	0
0	0	0	0	14	0	0	0	9	0	2	0
0	0	0	0	22	0	14	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	66	0	0	0	194	0	0	0
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
0	0	0	0	0	0	15	0	23	0	0	0
54	9	56	0	0	0	0	0	12	0	3	0
0	0	0	0	0	0	0	0	0	0	0	0
243	457	175	0	2	0	15	0	31	3	0	0
28	0	0	0	6	0	3	0	0	0	0	0
—	—	—	—	—	—	—	—	—	—	—	—
0	0	0	0	5	0	24	0	3	0	0	0
0	0	0	0	18	0	14	0	17	0	0	0
45	0	49	0	0	0	49	0	54	0	5	0
0	0	0	0	1	0	0	0	6	0	0	0
60	0	0	0	58	0	1	0	4	0	0	0
40	0	0	0	0	0	12	0	4	0	2	0
220	0	0	0	40	0	34	0	7	0	0	0
79	0	0	0	20	0	1	0	3	3	0	0
106	0	0	0	20	0	0	0	40	0	0	0
267	0	0	0	0	0	68	0	28	0	0	0
30	0	0	0	20	0	5	0	3	0	7	0
113	0	0	0	80	10	0	0	0	1	0	0
130	0	0	0	0	78	3	0	0	0	0	0
64	0	0	0	0	0	0	0	1	3	0	0
30	0	0	0	20	0	40	0	15	1	0	0
44	0	0	0	0	0	0	0	9	0	10	0
19	0	0	39	0	0	1	0	2	0	0	0
0	0	0	0	40	0	3	0	1	0	2	0
81	0	0	0	0	0	1	0	0	4	0	99
47	0	1,815	18	80	0	7	0	7	0	16	9
20	0	0	0	40	0	18	0	6	1	0	0
66	0	0	0	19	0	59	0	24	0	0	0
355	0	0	0	0	50	5	0	5	0	3	0
392	0	0	0	0	0	10	45	17	1	0	0
522	0	0	0	20	0	1	0	8	2	0	0
204	221	0	0	20	0	0	0	9	0	5	0
50	0	0	0	40	10	1	0	33	6	0	0
0	0	0	0	0	0	1	5	2	0	1	0
225	0	0	142	50	0	21	0	12	0	1	0

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Table 4. Group C. Yearlings & Adults. Worms recovered at autopsy

	Sheep No.	Date of birth	Date killed	*Trichostrongylus* spp. Fourth stage larvae	*T. colubriformis*	*T. falculatus*	*T. axei*	*T. vitrinus*	*T. pietersei*
DO	873	1958—1 September..	1960—26 April.......	3,279	1,648	1,058	0	2,110	0
O	881	2 September..	26 April.......	1,712	1,373	169	0	896	0
DO	813	8 July........	15 May........	0	0	0	0	0	0
DO	873	1 September..	10 May........	502	52	0	0	0	0
DO	891	6 October....	24 May........	10,719	1,750	1,800	1,780	0	0
	835	5 September..	24 May........	1,296	0	0	600	0	0
	813	30 August.....	7 June........	Discarded		—	—	—	—
	631	30 August.....	7 June........	1,340	200	0	540	0	0
DO	858	15 September..	21 June........	2,826	1,430	0	2,000	910	0
O	845	15 August.....	21 June........	1,780	0	0	720	0	0
DO	83	1 July........	5 July........	1,000	0	0	400	0	0
O	834	1 July........	5 July........	0	0	0	1,840	0	0
O	827	30 June.......	19 July........	350	0	0	351	0	0
O	818	30 June.......	19 July........	33	0	54	3,720	0	0
O	835	1 July........	3 August.....	518	4	0	4,034	0	0
O	89	1 July........	3 August.....	321	0	1,500	77	0	0
O	823	3 September..	17 August.....	233	330	0	167	0	0
DO	824	3 September..	17 August.....	722	660	0	2,830	0	0
O	822	3 September..	31 August.....	181	0	0	893	0	0
O	853	6 September..	31 August.....	238	0	0	1,366	0	0
O	821	3 September..	14 September..	100	0	0	1,140	0	0
O	834	5 September..	14 September..	500	0	250	3,460	0	0
O	968	1959—11 May.......	28 September..	655	2,760	0	1,136	400	0
O	932	13 September..	28 September..	203	2,190	0	2,334	1,220	0
O	34	1958—1 June.......	28 September..	248	1,860	0	635	773	0
O	977	1959—12 September..	12 October....	356	924	0	586	304	0
O	946	9 September..	12 October....	956	0	0	3,200	0	0
O	972	12 September..	26 October....	1,731	7,317	3,793	2,049	302	0
O	9107	18 September..	26 October....	7	1,080	2,381	144	1	645
O	926	6 September..	9 November..	89	99	0	289	0	0
O	999	16 September..	9 November..	727	1,799	1,320	908	66	29
O	935	8 September..	23 November..	0	0	0	14	0	0
O	933	14 September..	23 November..	Discarded		—	—	—	—
	5928	3 September..	7 December...	0	100	0	1,512	0	0
	5841	1958—10 September..	7 December...	1,531	0	0	0	0	0
	5924	3 September..	21 December...	24	166	1	0	0	0
	5945	1959—15 September..	21 December...	19	3	9	8	0	0
	5921	28 August.....	1961—4 January.....	Discarded		—	—	—	—
	5947	17 August.....	4 January.....	13	491	457	0	19	56
	5910	28 August.....	18 January.....	0	0	0	0	0	0
	5926	2 September..	18 January.....	0	20	0	0	0	0
	595	25 August.....	1 February...	208	0	0	0	0	0
	597	27 August.....	1 February...	0	320	0	160	0	0
	5920	3 September..	15 February...	0	0	0	0	0	0
	5942	12 September..	15 February...	0	10	0	0	0	0
	0957	10 September..	1 March......	0	0	0	0	0	0
	0989	14 September..	1 March......	0	0	0	0	0	0
	0921	5 September..	15 March......	850	472	939	217	0	0
	0975	12 September..	15 March......	225	80	0	86	0	0
	0916	5 September..	28 March......	135	1,359	775	89	0	0
	0997	16 September..	28 March......	153	726	1,492	138	0	0
O	9105	18 September..	12 April.......	1,198	749	891	103	45	39
	0923	5 September..	12 April.......	2,506	0	41	134	0	0
	5949	13 September..	26 April.......	130	694	553	147	91	0
	5933	4 September..	26 April.......	319	172	88	1,806	0	0
	594	25 September..	9 May........	86	409	690	97	68	68
	5931	4 September..	9 May........	368	88	0	91	0	0
	598	31 August.....	24 May........	253	104	104	144	0	0
	5932	4 September..	24 May........	367	2,461	915	264	300	195
K	5956	11 September..	7 June........	22	0	0	1,578	57	0
	5917	30 August.....	7 June........	902	3,945	1,362	1,982	271	276
	5915	30 August.....	22 June........	279	0	0	50	0	0
K	5961	13 September..	22 June........	89	40	0	130	0	0
O	9116	21 September..	6 July........	61	0	0	666	0	0
K	5948	10 September..	6 July........	0	0	0	45	0	0
	0987	14 September..	20 July........	20	0	0	0	0	0
K	5951	11 September..	20 July........	366	0	10	1,247	0	0
	5914	12 September..	3 August.....	439	0	0	143	0	0
	0995	16 September..	3 August.....	421	0	80	0	0	0
	0942	9 September..	16 August.....	Discarded		—	—	—	—
	0998	16 September..	16 August.....	219	177	0	892	89	0
	0966	11 September..	30 August.....	648	0	0	1,382	0	0
K	5921	4 September..	30 August.....	332	0	0	0	0	0

p193b

Table 4.—*Group C. Yearlings and adults. Worms recovered at autopsy* (cont.)

p193a p 193c

T. rugatus	*Ostertagia* spp. Fourth stage larvae	*O. circumcincta*	*O. trifurcata*	*O. ostertagia*	*Haemonchus* sp. Fourth stage larvae	*H. contortus*	*Cooperia* spp. Fourth stage larvae	*C. curticei*	*C. pectinata*	*C. punctata*	*C. spatulata*
1,076	6,900	1,150	0	0	240	400	0	425	0	0	0
0	1,428	2,380	0	0	0	70	0	115	0	0	0
0	1,728	700	210	0	0	0	252	52	0	0	0
0	174	600	0	0	0	0	0	0	0	0	0
3,900	1,668	1,340	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
—	—	—	—	—	—	—	—	—	—	—	—
0	0	270	0	0	0	0	0	400	0	0	0
0	910	1,550	0	0	0	0	116	450	0	0	0
0	0	180	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	200	0	0	1,523	0	0	0
0	205	271	0	0	50	10	0	0	0	0	0
0	266	413	0	0	0	0	0	110	0	0	0
0	382	2,016	222	0	94	0	0	14	0	0	0
0	206	644	72	0	0	0	0	1,667	0	0	0
0	133	133	0	0	0	0	0	300	0	0	0
0	836	0	0	0	0	0	25	150	0	0	0
0	166	1,800	200	0	0	166	166	183	0	0	0
0	355	1,185	0	0	0	0	116	166	0	0	0
0	0	160	0	0	0	16	0	960	0	0	0
0	25	200	0	0	5	0	250	500	0	0	0
0	40	1,842	138	0	300	157	0	0	0	0	0
0	616	3,392	344	0	0	225	0	0	0	0	0
0	836	3,104	325	0	1,770	190	550	656	0	0	0
0	1,199	877	83	0	0	395	200	0	0	0	0
0	214	2,260	220	0	848	356	0	0	0	0	0
0	1,597	1,974	257	63	655	421	0	0	0	0	0
0	25	189	27	0	2	36	0	1	0	0	0
0	929	282	0	0	22	18	15	60	0	95	0
0	704	798	91	34	83	244	0	0	0	29	0
0	15	108	24	0	0	90	0	0	0	0	0
—	—	—	—	—	—	—	—	—	—	—	—
0	0	2,088	0	0	0	0	133	0	0	0	0
0	1,208	0	0	0	387	0	0	0	0	0	0
0	17	7	10	0	0	127	0	84	0	0	0
0	13	53	28	0	2	33	0	0	0	0	0
—	—	—	—	—	—	—	—	—	—	—	—
0	0	91	27	0	0	706	0	0	0	0	0
0	0	14	3	0	0	229	0	0	0	0	0
0	0	79	0	0	0	272	0	0	0	0	0
0	0	248	0	0	105	1,296	52	934	566	1,198	0
0	0	90	0	0	0	1,633	0	866	0	0	0
0	72	57	0	3	528	401	0	0	0	0	0
0	60	139	38	22	60	550	0	0	0	0	0
0	0	0	0	0	1,250	275	0	0	0	0	0
0	105	12	0	0	240	215	0	0	0	0	0
0	654	4,345	905	0	1,960	0	0	79	78	315	79
0	1,240	450	0	0	206	118	1,060	300	0	0	0
0	707	1,086	134	0	2,003	521	110	75	0	150	0
0	746	2,816	733	0	1,055	1,065	0	0	0	0	0
0	80	2,695	307	0	3,009	302	0	0	0	0	0
0	789	164	41	0	175	0	0	0	0	0	0
0	458	128	0	0	4,459	0	0	78	77	77	0
0	815	544	86	0	868	0	41	115	58	172	0
0	320	3,709	868	0	480	2,336	3	136	499	0	0
0	977	694	81	0	2,469	280	0	526	186	657	44
0	245	1,435	104	0	2,538	621	50	1,750	0	1,262	778
0	166	265	53	0	3,323	52	18	1,223	0	0	450
0	0	0	0	0	52	0	0	350	0	0	350
0	1,787	187	31	0	6,816	0	0	407	0	1,763	136
0	313	100	0	0	477	0	0	0	0	0	0
0	569	0	0	0	0	0	0	40	0	0	0
0	48	338	200	32	231	2	0	140	0	0	0
0	15	0	0	0	0	0	20	240	0	0	0
0	62	157	0	0	523	80	0	370	0	0	0
0	600	1,542	607	0	867	319	0	954	0	0	106
0	113	3	0	0	16	0	0	2,760	0	0	458
0	428	536	57	0	225	47	19	330	0	0	80
—	—	—	—	—	—	—	—	—	—	—	—
0	404	365	46	0	1,023	385	8	577	0	0	0
0	637	721	93	76	218	380	15	0	0	0	1,060
0	166	495	0	0	12	0	0	300	0	0	0

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Table 4. Group C. Yearlings & Adults. Worms recovered at autopsy(cont)

p193b

Nematodirus spp. Fourth stage larvae	*N. spathiger*	*N. filicollis*	*Bunostomum* sp. Fourth stage larvae	*B. trigonocephalum*	*Oesophagostomum* sp. Fourth stage larvae	*O. venulosum*	*Chabertia* sp. Fourth stage larvae	*C. ovina*	*Trichuris globulosa*	*Trichuris parvispiculum*	*Strongyloides papillosus*
0	63	0	0	0	0	7	0	7	3	0	0
0	225	0	0	13	0	120	0	36	0	0	0
0	0	0	0	0	0	50	0	4	0	0	0
0	0	0	0	27	1	26	0	48	0	0	0
0	0	0	0	0	0	0	0	0	10	0	160
0	0	0	0	0	0	30	0	2	3	0	0
—	—	—	—	—	—	—	—	—	—	—	—
0	0	0	0	0	0	0	0	4	0	0	105
0	0	0	0	0	0	0	0	8	1	0	215
0	0	0	0	4	0	1	0	4	0	7	0
300	100	0	0	1	0	0	0	0	13	0	0
320	0	0	0	0	0	1	0	0	2	0	0
0	0	0	0	0	0	0	0	0	0	1	0
300	0	0	0	0	0	0	0	1	0	0	0
158	0	0	4	20	10	0	0	0	1	0	0
133	0	0	0	25	0	0	0	1	2	0	50
30	0	0	0	0	0	0	0	1	0	0	1,947
50	0	0	0	30	0	0	0	6	1	0	330
40	0	0	0	8	0	0	0	0	4	0	160
308	0	0	0	0	0	0	0	1	0	0	0
90	0	0	0	6	0	0	50	7	14	0	300
60	0	0	0	11	0	0	0	6	0	0	0
130	0	0	0	27	16	131	0	59	4	0	0
165	0	0	0	70	0	0	0	0	0	0	0
264	0	0	0	76	0	0	0	39	2	0	750
800	0	0	0	0	0	52	0	58	4	0	1,005
125	0	0	0	21	0	0	0	1	0	0	400
1,216	0	0	0	0	312	2	0	11	0	0	0
2	215	0	0	0	0	12	0	11	0	0	0
423	0	0	0	0	0	0	0	0	0	0	0
514	0	0	0	0	40	91	0	84	2	0	0
0	0	0	0	13	0	0	0	0	0	0	0
—	—	—	—	—	—	—	—	—	—	—	—
1,634	0	0	0	10	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	2	0	0	0
299	3	0	0	2	0	2	0	0	1	0	0
0	0	0	0	0	0	0	0	2	0	0	0
—	—	—	—	—	—	—	—	—	—	—	—
27	0	0	0	0	0	11	0	25	0	0	0
0	0	0	0	2	0	0	0	12	0	0	0
0	0	0	0	4	0	0	0	0	0	0	0
1,355	0	0	0	2	0	1	0	0	0	2	0
0	0	0	0	0	0	0	0	0	0	0	0
0	6	0	0	0	0	0	0	0	0	0	0
0	0	0	0	6	0	0	0	2	0	0	0
0	0	0	0	9	0	2	0	6	0	4	0
0	0	0	0	6	0	0	0	9	0	0	0
105	0	315	0	20	0	6	0	0	0	0	869
1,710	0	0	0	80	0	1	0	0	3	0	100
444	75	0	0	20	51	0	0	0	0	0	0
221	0	0	0	20	0	0	0	0	0	0	0
148	0	0	0	10	16	0	0	0	0	0	0
30	0	0	0	80	15	8	0	0	0	16	0
865	0	0	0	0	47	0	0	0	2	0	0
139	172	0	0	57	38	0	30	0	0	0	0
0	0	0	26	0	0	0	0	0	0	0	0
160	0	88	0	0	40	0	0	0	0	0	10
455	0	0	0	103	25	3	0	0	0	3	0
149	0	90	9	20	0	0	0	0	0	0	0
361	0	0	0	20	0	0	0	0	0	0	0
136	0	0	0	0	0	1	0	3	0	0	0
1,941	0	0	0	3	0	0	0	0	1	0	0
752	0	0	0	0	0	0	0	0	0	1	40
240	0	0	0	40	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	2	4	0	0
140	0	0	0	20	0	0	0	0	0	1	370
150	0	0	17	0	0	0	0	21	0	0	0
1,138	0	0	0	20	0	0	0	0	0	0	115
427	0	0	0	20	0	0	0	0	0	0	0
—	—	—	—	—	—	—	—	—	—	—	—
126	0	0	0	70	0	39	0	7	0	0	0
264	0	0	0	20	0	0	0	1	0	0	0
8	0	0	0	20	0	0	0	0	0	0	0

TABLE 5.—*The proportions of immature and sexually mature* Trichostrongylus *spp.*

Sheep No.	Date of slaughter	Immature		Mature	
		Female	Male	Female	Male
		Group A			
K6036......	12 April.......	35	25	44	18
K6035......	12 April.......	38	11	128	103
6017......	26 April.......	48	24	30	21
6022......	9 May.......	40	3	65	42
0031......	24 May.......	22	10	63	53
0037......	7 June.......	32	5	78	52
0038......	22 June.......	10	0	22	22
0048......	20 July.......	10	3	0	0
0055......	3 August.....	50	21	13	6
	Total...........	285	102	443	317
	Grand Total....	387		760	
	Average........	33·7%		66·3%	
		Group B			
0022......	12 April.......	46	4	25	43
0021......	12 April.......	31	2	0	0
6029......	9 May.......	9	4	44	82
0024......	24 May.......	39	5	57	12
0025......	24 May.......	69	12	57	30
0027......	7 June.......	7	9	43	26
0026......	7 June.......	87	38	30	19
K6047......	22 June.......	78	8	22	8
0028......	22 June.......	9	3	73	63
0029......	6 July.......	25	2	47	2
K6048......	6 July.......	0	0	2	0
0030......	20 July.......	40	20	34	26
6031......	3 August.....	10	78	17	51
6030A....	3 August.....	52	12	20	31
6033......	31 August.....	13	4	73	66
6032......	31 August.....	58	4	13	34
	Total..........	573	205	557	493
	Grand Total...	778		1,050	
	Average.......	42·6%		57·4%	
		Group C			
09105.....	12 April.......	47	21	41	19
594.....	9 May.......	32	2	22	20
	Total..........	79	23	63	39
	Grand Total...	102		102	
	Average.......	50·0%		50·0%	