Onderstepoort J. vet. Res. 44 (4), 261–270 (1977)

PARASITES OF DOMESTIC AND WILD ANIMALS IN SOUTH AFRICA. IV. HELMINTHS IN SHEEP ON IRRIGATED PASTURE ON THE TRANSVAAL HIGHVELD

I. G. HORAK(1) and J. P. LOUW(2)

ABSTRACT

HORAK, I. G. & LOUW, J. P., 1977. Parasites of domestic and wild animals in South Africa. IV. Helminths in sheep on irrigated pasture on the Transvaal Highveld. *Onderstepoort Journal of Veterinary Research,* 44 (4), 261–270 (1977).

The seasonal incidence of helminth infestation in sheep on newly established irrigated pastures was determined by the slaughter of pairs of tracer lambs exposed for periods of approximately 33 days from October 1968–July 1970 and of sets of 3 lambs from March 1971–May 1973.

It took several months for the infestation to become established on the pasture, but thereafter, of the various species present, *Haemonchus contortus* was most prevalent. In general, peak burdens of this species were recovered from January–May or June, while marked inhibition of larval development was evident from April–August. *Ostertagia circumcincta* usually occurred in increased numbers from April–October, and larval development was inhibited during July and August. Although the sizes of the burdens varied considerably from year to year, *Trichostrongylus* spp. were present mainly from April–August.

Oesophagostomum columbianum, although present in the lambs slaughtered during the first 5 months of the survey, virtually disappeared until May 1971. After this it reappeared in small numbers in nearly all the sheep, reaching peak burdens during April and May 1972, and May 1973.

Moniezia expansa were generally recovered from the lambs slaughtered from November–May.

Résumé

PARASITES DES ANIMAUX DOMESTIQUES ET SAUVAGES EN AFRIQUE DU SUD. IV. HELMINTHES DU MOUTON SUR PÂTURAGES IRRIGUÉS DES HAUTS PLATEAUX DU TRANSVAAL

On a déterminé l'incidence saisonnière de l'infestation helminthique du mouton, sur des pâturages irrigués d'établissement récent, en sacrifiant des paires d'agneaux indicateurs exposés pour des périodes d'environ 33 *jours d'octobre* 1968 *à juillet* 1970*; de mars* 1971 *à mai* 1973 *on a utilisé* 3 *agneaux chaque fois.*

L'infestation demande plusieurs mois pour s'installer dans les pâturages mais une fois ce délai passé, c'est Haemonchus contortus *qui, des diverses espèces présentes, est la plus commune. De façon générale, cette espèce a présenté les charges les plus fortes de janvier à mai ou juin, tandis que d'avril à août il y avait une nett inhibition du développement larvaire. Les quantités d'*Ostertagia circumcincta *allaient habituellement croissant d'avril à octobre, et le développement larvaire était inhibé en juillet et août. Malgré une variation annuelle considérable de l'ampleur des charges, les diverses espèces de* Trichostrongylus *se sont principalement manifestées d'avril à août.*

Oesophagostomum columbianum *se rencontrait chez les agneaux sacrifiés pendant les 5 premiers mois de l'enquête, mais disparut ensuite presque complètement jusqu'en mai* 1971. *Après quoi il a fait sa réapparition en petites quantités chez presque tous les moutons, atteignant des charges maximales en avril-mai* 1972 *et en mai* 1973.

De façon générale, on a retrouvé Moniezia expansa *chez les agneaux sacrifiés de novembre à mai.*

INTRODUCTION

The seasonal incidence of parasitic helminths of sheep based on worm counts at slaughter was investigated in the summer rainfall areas of the Cape Province of South Africa by Barrow (1964) and Rossiter (1964), by Snijders, Stapelberg & Muller (1971) in a non-seasonal rainfall area, and by Viljoen (1964, 1969) in the semi-arid districts of the Cape Province, but not in the other provinces or on irrigated pastures. Large numbers of sheep throughout the country are kept on irrigated pastures and the effect of this method of husbandry on helminth epizootiology is an important factor in any control programme.

The present paper describes 2 helminth surveys conducted in sheep grazed on irrigated pastures in a summer rainfall area at Hennops River in the Pretoria district of the Transvaal Highveld.

MATERIALS AND METHODS

SURVEY 1

Pastures

The grazing at Hennops River (25°50'S; 27°58'E; Alt. ±1 280 m) consists of grass/clover leys established in 1967 and 1968 and is divided into summer and winter pastures.

(1) Department of Parasitology, Faculty of Veterinary Science, University of Pretoria, P.O. Box 12580, Onderstepoort, 0110
(2) MSD Research Centre, Hennops River, Private Bag X3, Halfway House, 1685

Received 12 September 1977—Editor

The summer grazing comprises 10 fields, each approximately 0,3 ha in area and bounded by slightly raised contour walls, and the winter grazing, a single pasture approximately 1 ha in area.

Infestation and management

Helminth infestation was introduced on to the newly established summer pasture by a flock of 30 Dorper sheep and 115 Merino ewes. The pasture was grazed from April 1968–January or February 1969, during which time the Merinos lambed.

Seventy-eight weaned Merino lambs, henceforth referred to as flock lambs, were left on the pasture after the other animals had been removed. Forty-one of these lambs received a daily low level dosage of thiabendazole incorporated in feed pellets, while the remaining 37 lambs received only feed pellets. Feed pellet and anthelmintic administration ceased in November 1969. The lambs used in the seasonal incidence survey grazed with this flock of lambs during the day and were housed at night with the lambs that received the unmedicated feed pellets.

All the lambs grazed in a single movable pen enclosing approximately 0,06 ha of pasture. When the vegetation within the pen had been depleted, the pen was moved to an adjacent strip of pasture. Five of the 10 fields of summer pasturage were grazed in this way.

In May 1969, when the sheep were moved to the recently established but hitherto ungrazed winter pasture, the movable pen was erected on the winter and summer pasture on alternate days for a period of 2 weeks. During this period, whenever the pen was placed on the winter pasture, it was erected on a strip adjacent to that previously grazed so that contamination was spread over a large area of the pasture. The sheep remained on the winter pasture until the end of September 1969.

From May–October 1969, 2 of the 5 fields of summer pasture previously grazed by the sheep were grazed by calves in a helminth survey (Horak & Louw, in press). Amongst other nematodes these calves were infested with *Cooperia pectinata* and *Cooperia punctata*.

In October 1969, the sheep were moved from the winter pasture on to one of the fields grazed by the calves, the above system of alternate day grazing being used. From November 1969 until the end of the survey in July 1970, the sheep had grazed 3 of the 5 fields utilized during the previous summer, but did not graze again those fields on which the calves had been penned.

On 13 March 1970, 18 worm-free Merino lambs were added to the experimental flock and were removed in April 1970 after 47 days on the pasture. In May 1970, 14 worm-free Karakul weaner lambs were added to the flock and were still present at the conclusion of the trial.

The pastures were irrigated by means of sprinklers on 2–4 occasions each month, approximately 37 mm of water being supplied on each occasion. Fertilizer was applied when required.

Tracer lambs

The tracer lambs were born and raised under worm-free conditions and were 4–8 months old when placed on the pasture. From October 1968–June 1970 they were introduced on to the pasture in pairs at approximately 28-day intervals, and removed approximately 33 days later, thus allowing an overlap of 5 days between successive pairs. After removal from the pasture, the lambs were starved under worm-free conditions for 48 hours and then slaughtered.

Flock lambs

At approximately 14-day intervals faeces were collected from 20–25 lambs for worm egg counts and faecal cultures. Faecal sampling was extended to monthly intervals from November 1969–May 1970.

Slaughter and counting techniques

At slaughter the lungs and gastro-intestinal tracts were processed for worm recovery in a waterbath, using modifications of techniques described by Shone & Philip (1967), Reinecke (1967) and Anderson & Verster (1971). The mucosae of the gastro-intestinal tracts were scraped and the mucosal scrapings subjected to pepsin/HCl digestion. When *Moniezia expansa* were present, the strobila were removed from the opened small intestine.

Burdens were calculated by counting the worms in total collections and in representative samples. Scolices were counted to determine the number of cestodes present.

General

Minimum and maximum temperatures and rainfall were recorded daily, as also the approximate amount of water supplied by irrigation, the number of applications per month and the fertilizer applications.

SURVEY 2

Pastures

During the entire survey period only 4 of the 10 fields of summer grazing mentioned in Survey 1 were utilized.

Infestation and management

Five of the lambs belonging to the "flock" in Survey 1 continued to graze these fields from the conclusion of that survey and served to seed and maintain infestation on the pastures.

Of the 40 lambs put out to pasture during January 1971, 8 were not treated with an anthelmintic during their sojourn on the pastures, while the remainder were drenched at various intervals. These lambs were removed in batches during the period April–July 1971.

Six lambs, artificially infested with *Chabertia ovina*, were placed on the pastures during July 1971, but 5 of these subsequently died. During August, September and October 1971, the number of untreated "seeder" sheep was increased to 23. This number was gradually decreased, however, until only 8 sheep remained at the conclusion of the survey in May 1973. During November 1971, a further 12 sheep were pastured until January 1972. Of 4 untreated Angora goat kids placed on the pasture in May 1972, 3 survived until the conclusion of the survey. During September 1972, approximately 70 Merino lambs were put out with the survey sheep on the pasture and remained there until the end of the survey. These lambs were treated with anthelmintics at various intervals.

From February–7 July 1971, worm egg counts were done at weekly intervals on the faeces of the 8 untreated lambs in the group of 40 lambs. Thereafter, faecal worm egg counts were done at weekly intervals until September 1972 and then at 2-weekly intervals on some of the "seeder" sheep. On each occasion the faeces of the sheep were combined and a single faecal larval culture made. From these the mean monthly total and differential egg counts were calculated.

All the sheep were confined in a movable pen which was shifted to an adjacent strip of pasture whenever the enclosed vegetation had become depleted. The sheep were housed daily from approximately 17h00–07h00 the following morning, as a precautionary measure against theft.

Irrigation and fertilizer were applied as in the previous survey.

Tracer lambs

Successive sets of 3 lambs were exposed, slaughtered and processed for worm recovery in the same way as in Survey 1.

RESULTS

SURVEY 1

Tracer lambs

The mean worm burdens of the tracer lambs are summarized in Table 1.

Haemonchus contortus: Peak burdens of predominantly early 4th stage larvae were recovered from the lambs slaughtered from March–May 1969 and from February–June 1970. Adult burdens reached a peak from November 1969–March 1970.

Ostertagia spp: Both *Ostertagia circumcincta* and *Ostertagia trifurcata* were present, peak total burdens being recorded generally during April, May or June and September and October.

TABLE 1 The mean worm burdens of the tracer lambs in Survey 1

Date slaughtered	Mean numbers of helminths recovered at necropsy												
	H. contortus		*Ostertagia* spp.		*T. colubriformis*		*N. spathiger*		*Cooperia* spp.	*O. columbianum*	*Trichuris* spp.	*D. filaria*	*M. expansa*
	4th	Adult	4th	Adult	4th	Adult	4th	Adult	Total	Total	Total	Total	Scolices
1968													
27 Nov.	54	41	254	49	12	30	5	2	0	4	0	5	0
24 Dec.	1	85	56	121	0	24	2	7	0	30	0	12	0
1969													
23 Jan.	5	28	19	24	5	8	3	1	0	3	0	0	0
19 Feb.	69	8	42	9	44	25	1	1	0	8	0	0	0
19 Mar.	1 067	84	121	38	0	12	4	5	0	1	0	0	6
16 Apr.	4 668	0	164	5	1	0	4	0	0	0	1	0	6
9–14 May.	6 099	13	203	86	2	34	2	8	0	0	3	1	4
11 Jun.	203	3	0	2	0	2	6	2	0	0	0	0	5
9 Jul.	0	0	1	6	0	0	0	0	0	0	1	0	1
6 Aug.	2	13	15	114	0	6	0	0	0	0	0	4	6
5 Sep.	0	2	1 102	509	0	5	3	2	2	0	2	2	0
1 Oct.	10	1	112	357	8	5	12	2	25	0	2	3	1
29 Oct.	85	8	6	3	0	0	5	2	2	0	0	0	0
26 Nov.	2	519	24	398	0	13	0	2	4	0	0	0	15
24–29 Dec.	347	1 047	18	39	1	8	1	5	35	3	0	0	64
1970													
22 Jan.	825	271	44	40	1	14	1	1	21	0	3	0	44
19 Feb.	2 507	1 653	120	132	3	107	3	7	0	0	2	0	202
19 Mar.	1 237	561	0	6	3	90	2	6	6	0	2	0	20
19–28 Apr.	2 494	225	43	62	3	524	4	6	12	0	0	6	19
20 May.	1 644	20	72	163	6	762	30	46	44	1	2	14	16
19 Jun.	1 464	36	513	169	43	1 156	152	30	0	0	34	81	4
24 Jul.	69	8	64	51	1	201	100	78	0	0	1	55	1

4th—Fourth stage larvae. Lambs slaughtered on different dates in the same month

Trichostrongylus colubriformis: Reached peak burdens from April–June 1970.

Cooperia spp: Both *C. punctata* and *C. pectinata* were recovered in small numbers from September 1969–May 1970.

Nematodirus spathiger: Peak burdens were recovered during May–July 1970.

Oesophagostomum columbianum: This species virtually disappeared after the first 5 months of the survey.

Dictyocaulus filaria: Worms of this species were present in small numbers at the start and during the survey. From April–July 1970, however, they increased markedly.

Moneizia expansa: Peak burdens were recovered from the lambs slaughtered from November 1969–May 1970.

Flock lambs

The mean monthly differential faecal worm egg counts of the untreated lambs, the atmospheric temperature and monthly precipitation on the pastures are graphically represented in Fig. 1.

Except in December 1969, when *Ostertagia* spp. predominated, the rise and decline in the mean total egg counts were due to fluctuations in the egg output of *H. contortus.* These counts reached a peak during March 1969, declined in April, rose again in May and fell markedly thereafter. In March 1970 a major peak of 7 021 e.p.g. was reached and this fell to zero during May of the same year.

Ostertagia spp. reached peak egg output during March, September and December 1969, and January 1970.

Peak egg counts for *Trichostrongylus* spp. were recorded during March and December 1969 and March and May 1970.

The larvae of *S. papillosus* were recovered from faecal cultures during January and May 1969, those of *Cooperia* spp. during December 1969 and January 1969 and May 1970. *Nematodirus spathiger* eggs were present in the faeces during March 1969 and 1st stage *D. filaria* larvae were recovered from the faeces during January, February and July 1969.

Mean monthly minimum temperatures below 6 °C were recorded during July and August of 1969, and June and July 1970, and mean maximum temperatures exceeding 28 °C were recorded during November and December 1969, and January 1970.

The lowest monthly total amount of water supplied to the pasture as rainfall and irrigation was 101 mm during October 1968, while, during February, April and December 1969, the monthly totals exceeded 200 mm.

SURVEY 2

The mean worm burdens of the tracer lambs are summarized in Table 2, while Fig. 2 gives the monthly mean differential faecal worm egg counts of the "seeder" sheep, atmospheric temperature, rainfall and irrigation on the pastures.

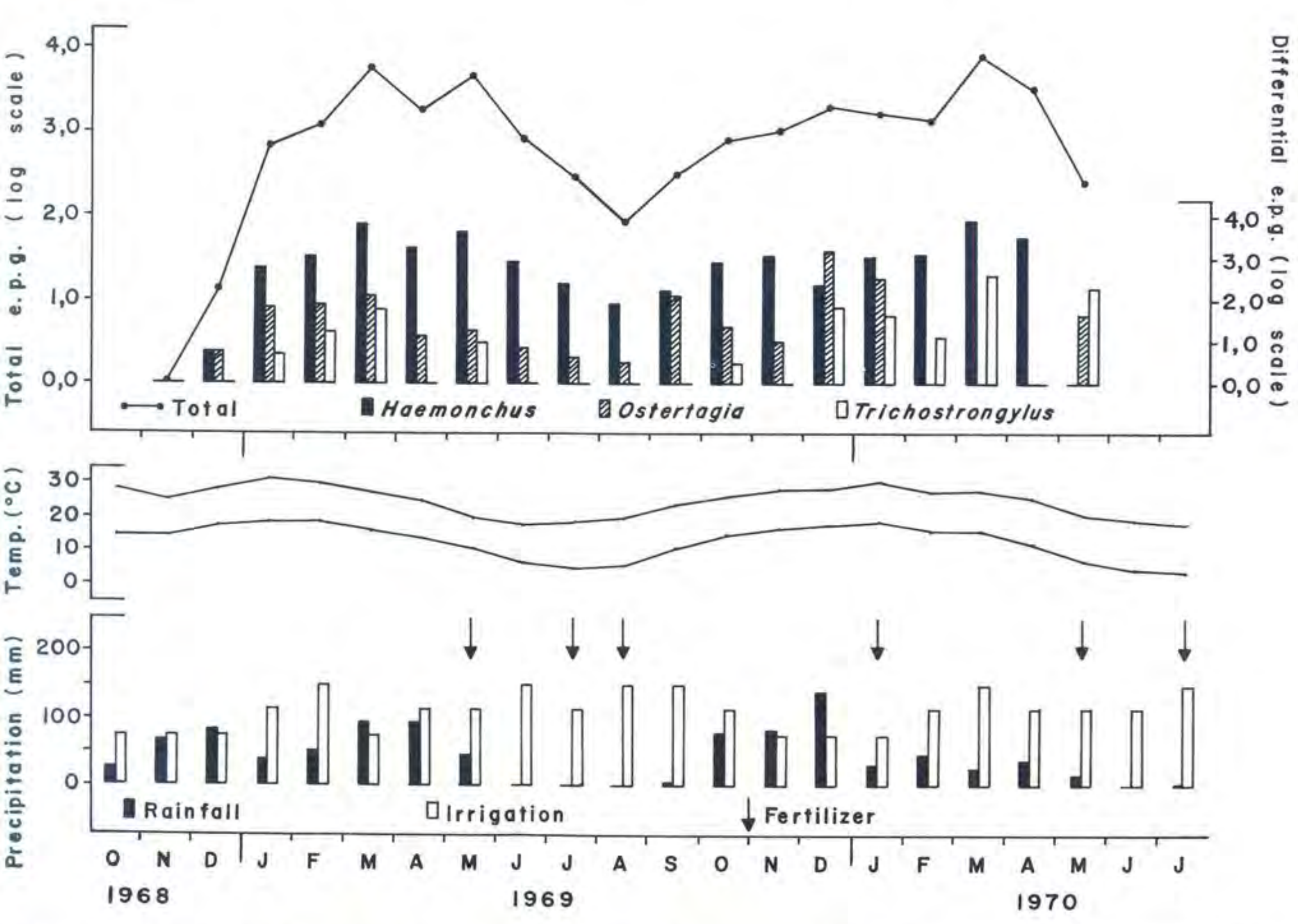

FIG. 1 Survey 1. Total and differential faecal worm egg counts of the untreated flock lambs, atmospheric temperature, rainfall, irrigation and fertilizer applications on the pastures

TABLE 2 The mean worm burdens of the tracer lambs in Survey 2

Date slaughtered	Mean numbers of helminths recovered at necropsy													
	H. contortus		*O. circumcincta*		*Trichostrongylus* spp.		*N. spathiger*		*S. papillosus*	*O. columbianum*		*C. ovina*	*Trichuris* spp.	*M. expansa*
	4th	Adult	4th	Adult	4th	Adult	4th	Adult	Adult	4th	Adult	4th or 5th	Total	Scolices
1971														
23 Apr.	2 897	826	102	120	3	117	1	2	0	0	0	0	0	20
21 May	3 908	866	111	415	13	397	2	4	13	3	6	0	2	74
18 Jun.	1 130	67	61	75	9	128	1	4	0	1	1	0	2	1
16 Jul.	479	39	126	101	0	305	2	6	0	0	8	0	2	0
13 Aug.	389	56	148	219	10	190	8	12	0	0	0	0	7	5
13 Sep.	48	19	5	57	0	7	0	12	0	0	3	0	0	16
8 Oct.	5	20	32	236	3	104	32	71	0	1	0	0	1	18
8 Nov	1	3	5	98	2	187	30	53	0	1	1	0	3	249
6 Dec.	279	331	70	239	2	230	4	11	0	17	4	0	6	13
29 Dec.	16	134	9	16	2	107	1	0	5	4	8	1	2	23
1972														
31 Jan.	305	586	22	35	14	146	1	7	12	2	1	1	8	2
25 Feb.	21	124	0	14	2	15	0	2	1	1	1	0	1	18
24 Mar.	415	62	70	67	0	290	0	0	2	2	1	0	0	1
21 Apr.	2 140	258	798	442	520	1 937	5	16	0	132	21	0	6	67
19 May	1 876	51	1 125	1 162	212	4 438	22	0	10	163	108	3	5	48
16 Jun.	51	13	214	227	29	641	3	2	0	10	0	1	1	2
14 Jul.	83	8	1 827	620	63	602	43	8	3	6	11	1	0	4
11 Aug.	134	46	1 952	517	33	643	15	36	0	1	2	0	0	1
8 Sep.	6	14	275	274	15	41	23	28	1	0	1	1	3	1
6 Oct.	12	1	728	2 528	5	490	114	9	0	1	1	1	0	0
3 Nov.	16	6	25	308	15	263	34	1	0	3	1	0	0	156
30 Nov.	7	151	1	40	1	41	2	1	178	1	0	0	0	122
29 Dec.	207	50	1	6	8	15	1	2	3	1	0	0	2	1
1973														
26 Jan.	84	583	4	50	4	256	0	2	0	1	1	0	8	34
23 Feb.	802	124	40	11	33	132	1	3	1	4	0	0	0	408
23 Mar.	109	792	0	7	6	125	0	4	7	2	1	0	0	56
19 Apr.	5 579	18	0	2	243	484	0	1	15	15	2	0	2	1
18 May	5 678	324	0	13	68	863	0	0	0	35	8	0	5	1

4th—Fourth stage larvae

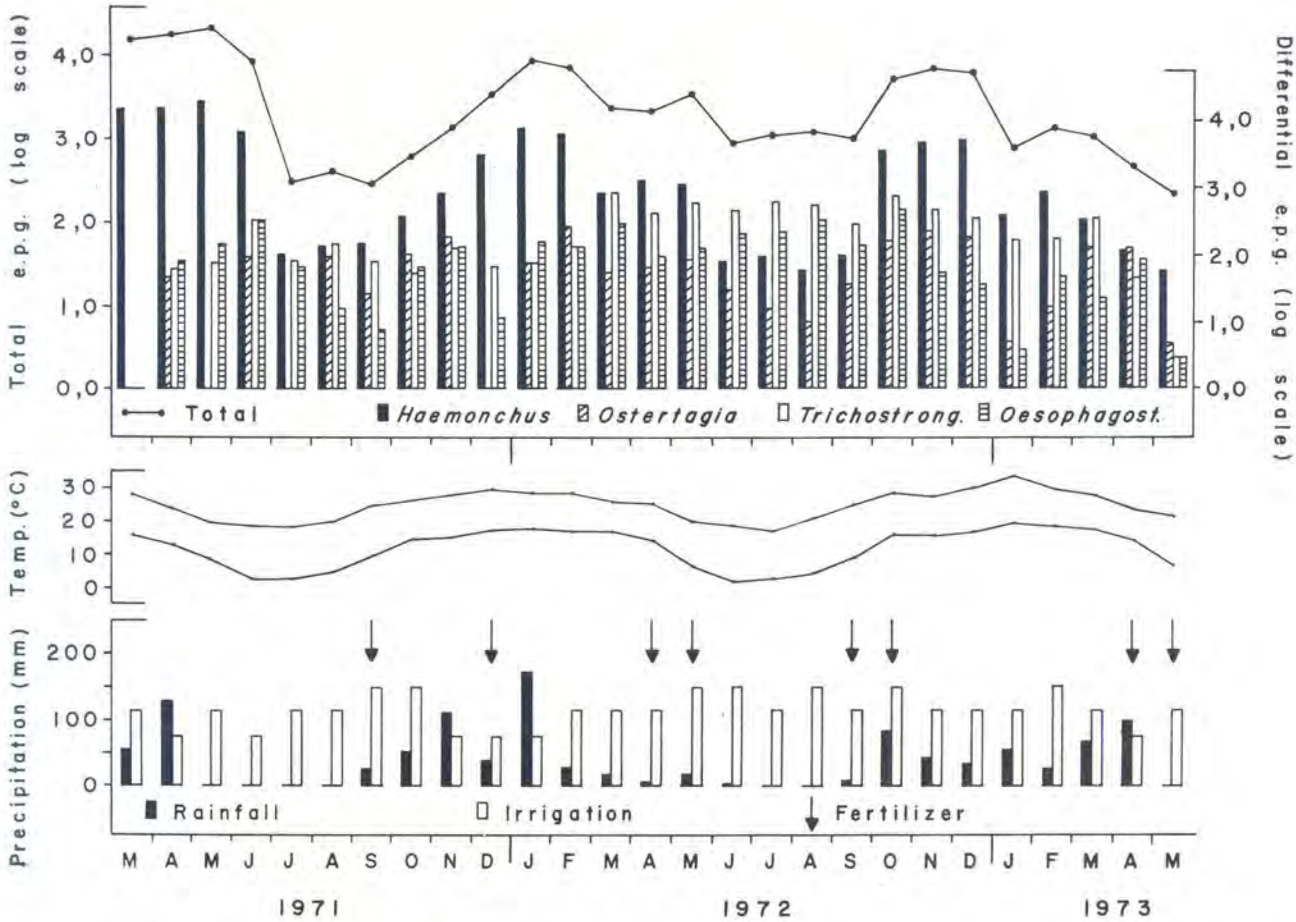

FIG. 2 Survey 2. Total and differential faecal worm egg counts of the seeder sheep, atmospheric temperature, rainfall, irrigation and fertilizer applications on the pastures

The mean monthly burdens of *Haemonchus contortus, Ostertagia circumcincta, Trichostrongylus* spp. and *M. expansa* recovered from the lambs slaughtered in Surveys 1 and 2 and the percentage of worms of the first 2 species in the 4th stage of larval development are summarized in Table 3.

Haemonchus contortus: Peak burdens of predominantly early 4th stage larvae were recovered from the lambs slaughtered during April and May in each year of Survey 2. Peak burdens of adult worms were recorded during April and May 1971, January 1972 and January and March 1973.

Peak faecal worm egg counts were recorded from the sheep which served as "seeders" during March–May 1971, January and February, and November and December 1972 (Fig. 2).

The mean percentage of worms in the 4th stage of development increased from 43,8% during January until it reached 95,6% during June. Thereafter, it decreased to 10,1% in November and rose to 36,6% in December (Table 3).

Ostertagia circumcincta: Peak levels in total worm burden were generally encountered in the lambs slaughtered from April–October. During 1973 the worm burdens remained at a particularly low level until the conclusion of the survey.

Peak faecal worm egg counts were recorded in the "seeder" sheep during October and November 1971, February and October–December 1972 and during March and April 1973.

The mean percentage of worms in the 4th stage of development increased from 38,0% during January to 72,5% during July and August.

Trichostrongylus spp: *Trichostrongylus colubriformis, Trichostrongylus falculatus* and *Trichostrongylus rugatus* were recovered, but the exact number of each species was not determined. Peaks in total worm burdens were encountered from April–August in each year of the survey.

The faecal worm egg counts of the "seeder" sheep reached a peak during June 1971, March–December 1972 and during March 1973.

Nematodirus spathiger: Total mean burdens never exceeded 123 worms, but within the limits of this number peak burdens were recovered from the lambs slaughtered during October and November 1971 and October 1972.

Oesophagostomum columbianum: Peak total worm burdens were recovered from the lambs slaughtered during April and May 1972, and May 1973.

The "seeder" sheep had peak faecal worm egg counts during May and June 1971, January–March and June–October 1972.

Moniezia expansa: The eggs recovered from gravid segments indicated that *M. expansa* was the only species present as gravid worms, but no specific identification was attempted if there were no gravid segments present.

TABLE 3 The mean monthly worm burdens of tracer lambs slaughtered at Hennops River 1968–73

Month	Total No. of sheep slaughtered	Mean worm burdens					
		H. contortus		*Ostertagia* spp.		*Trichostrongylus* spp.	*M. expansa*
		Total	% 4th stage	Total	% 4th stage	Total	Total
Jan.	9	696	43,8	59	38,0	117	18
Feb.	10	1 168	65,2	80	55,3	90	168
Mar.	10	1 003	61,6	86	63,6	147	22
Apr.	13	3 840	92,5	380	63,0	843	24
May	13	4 127	92,9	733	44,7	1 506	31
Jun.	10	720	95,6	310	59,7	482	3
Jul.	10	198	92,1	826	72,5	331	2
Aug.	8	238	82,6	1 106	72,5	330	4
Sep.	8	33	60,8	632	60,2	25	6
Oct.	10	32	75,2	1 152	21,8	183	6
Nov.	13	137	10,1	221	22,5	126	124
Dec.	13	462	36,6	114	26,0	89	18

Cestode burdens varied considerably between individual lambs but the largest numbers were generally recovered from lambs slaughtered from October–May. The greatest number of scolices recovered from a single lamb was 788.

Rainfall was generally low or absent from May–September, but with irrigation the total monthly precipitation on the pastures always exceeded 100 mm except during June 1971 when it dropped to approximately 75 mm.

In each year regrowth of the pastures slowed down during April and virtually ceased during May. It commenced again during September and was excellent from October onwards.

Discussion

During both surveys, virtually the same pastures, periods of exposure of tracer lambs and methods of helminth recovery were utilized. The provision of moisture to the pastures by means of regular sprinkler irrigation largely countered the usual variation in monthly rainfall. It was thus possible to combine the findings of the surveys and determine the mean seasonal occurrence of helminths on the pastures at Hennops River. Table 3 is a summary of these findings for the 4 major genera.

The fact that the sheep were starved for 48 hours prior to slaughter and the helminths recovered at necropsy were thus 2–35 days old, must be taken into consideration when an estimate is made of the percentage of 4th stage worms which should theoretically be present.

Haemonchus contortus

In this species, the 3rd moult occurs $1\frac{1}{2}$ days and the 4th moult from 9–11 days after infestation (Veglia, 1915). Supposing that the same level of infestation was acquired daily from the pastures, there should, theoretically, be few 3rd stage larvae in the tracer lambs at slaughter and 4th stage larvae should account for 7/33 (21,2%) of the worm burden. Except during November, when 4th stage larvae comprised only 10,1% of the total infestation, the percentage of worms in this stage of development always exceeded 36% (Table 3).

From April–July more than 90% of the worms were in the 4th larval stage of development. This retardation in the 4th stage was not dependent upon the magnitude of the total burden of *H. contortus*, for, while the highest burdens of this species were recorded during April and May, the degree of retardation during July, when the total burden was considerably lower, was as high. These findings are in general agreement with those of Southcott, Major & Barger (1976) in New South Wales except that they recovered peak numbers of *H. contortus* from tracer lambs grazed during January–March, that is, prior to the onset of maximum larval retardation.

The phenomenon of arrested development, reviewed by Michel (1974), accounts for this extension of the life cycle in the 4th larval stage and ensures that the parasite survives unfavourable external environmental conditions in a favourable internal habitat in which it can develop to maturity once the external conditions are more suitable. This phenomenon has been described in *O. circumcincta* infestations in sheep by James & Johnstone (1967), Connan (1971) and Reid & Armour (1972), and in *H. contortus* by Muller (1968), Connan (1971), Blitz & Gibbs (1972), Brunsdon (1973) and Waller & Thomas (1975), and possibly corresponds to diapause in insects as suggested by Armour & Bruce (1974).

As the winter conditions at Hennops River are not severe, the development of *H. contortus* is not completely inhibited as it is in countries where the winters are cold (Connan, 1971; Blitz & Gibbs, 1972; Waller & Thomas, 1975). Nevertheless the prolonged period of hypobiosis from February–October severely limits the potential number of generations in a year.

A further factor in the prolongation of the period of generation is the apparent time-lag between maximum contamination of the pastures with eggs and the subsequent availability of larvae. During 1971, maximum faecal worm egg counts were recorded in the 8 untreated lambs during March–May and maximum *H. contortus* burdens in the tracer lambs during April and May. Maximum worm egg counts of the actual "seeder" sheep, were not recorded until January and February 1972, and again during November and December of the same year, while maximum worm burdens in the tracer lambs were only encountered during April and May of 1972 and 1973. Thus maximum contamination of the pastures with *H. contortus* eggs preceded maximum larval availability by several weeks. Similar observations were made in N. E. England by Waller & Thomas (1975), while Southcott *et al.* (1976) found that summer contamination of pastures in New South Wales was rapidly translated into peak worm burdens in tracer lambs. The increase in worm burden during autumn in this survey, however, may be because pasture regrowth declined and ceased during April and May and consequently the number of larvae per kg of herbage increased. It could also be because more 1st and 2nd stage larvae survived because of the cooler conditions and thus more 3rd stage larvae became available. The decrease in temperature in June and subsequent months prevented further development of *H. contortus* larvae and thus further pasture contamination.

The delay between contamination and infestation, combined with the prolonged period of arrested development, could mean that certain worms would complete only one generation a year, an observation made by Connan (1971) in S. England and Waller & Thomas (1975) in N. E. England. Other worms, less prone to inhibition, could complete 2 or more generations a year. This variation in arrested development in strains within a population has been discussed by Michel (1974).

In the flocks lambs and "seeder" sheep, self-cure of *H. contortus* infestation occurred in May 1970, July 1971, March and June 1972 and January 1973. The rise in egg counts during October and November 1969 and 1971 was probably due to the maturation of overwintering-, or immunologically retarded larvae later reinforced by the ingestion of fresh infestation from the grazing. During 1972, the egg counts recorded before December were probably entirely due to the maturation of overwintering larvae as very little new infestation was acquired from the pastures at this time (Table 2). The ingestion of the first substantial numbers of infective larvae during January 1973 (Table 2), however, resulted in self-cure which effectively depressed egg counts due to *H. contortus* for the remainder of Survey 2.

Ostertagia spp.

Ostertagia circumcincta undergoes the 3rd moult 3 days after infestation and the 4th moult, 6 days later (Denham, 1969). Thus, at slaughter, the tracer lambs should have harboured a few 3rd stage larvae (these were not recovered, however, possibly because the techniques used were not sensitive enough), 4th stage larvae and adult worms. Provided equal numbers of larvae had been acquired on a daily basis, the 4th larval stages should have accounted for 6/33 (18,2%) of the total population at slaughter.

A ratio of immature to adult worms approximating the above percentage was recorded in the sheep slaughtered from October–December (Table 3). At all other times, the greater percentage of worms in the 4th stage of development indicated retardation. The degree of retardation in the 4th stage was not dependent upon the number of worms present, for, though in August and October the mean total worm burdens were practically identical, the highest and lowest percentages of arrested development were recorded in these months respectively.

Arrested development in *Ostertagia* spp. infestations occurred later in the autumn and ceased sooner in the spring than the same phenomenon in *H. contortus*. The degree of retardation was not as great as in *H. contortus* and maximum retardation was only encountered during July and August.

As can be seen from the mean total worm burdens in these surveys and the results of Muller (1968), Anderson (1972; 1973) and Southcott *et al.* (1976), *O. circumcincta* in the southern hemisphere favours the cooler months of the year from autumn until spring for development on the pastures. Because of this natural preference for cooler conditions, the pressure to overwinter as inhibited 4th stage larvae will be lower and will occur later than for *H. contortus* which in these surveys preferred the warmer months from December–May for development on the pastures. Where the climate is colder, however, as in Cambridge, England, the greater overwintering pressure results in the virtual cessation of development during the winter months (Connan, 1971).

When these factors are taken into consideration, it is probable that, under the climatic and management conditions prevailing at Hennops River, the generation time of *Ostertagia* spp. is shorter than that of *H. contortus*. The relatively small number of eggs laid by the female worms (Kauzal, 1933) and the warm summers, however, probably preclude a major role for this nematode.

The particularly warm weather experienced during December 1972 and January 1973 probably played a considerable role in reducing the *O. circumcincta* infestation available to the tracer lambs in 1973. The "vacuum-cleaner" effect of the large numbers of other lambs grazing the pasture at this time must also be borne in mind. Although these lambs were probably ingesting substantial numbers of larvae they were contributing little to further pasture contamination as they were treated with anthelmintics at 4-weekly intervals.

Trichostrongylus spp.

In Survey 1, only *T. colubriformis* was recovered, while, in Survey 2, this species and *T. falculatus* and *T. rugatus* were encountered.

No pattern of retardation in the 4th larval stage could be discerned in these parasites at any time during the year. Muller (1968), however, has suggested that *Trichostrongylus* spp. overwinter in the 5th stage but, as no attempt was made in this trial to differentiate 5th stage from adult worms, no conclusions on this postulation can be drawn.

The peak *Trichostrongylus* spp. worm burdens encountered during April and May of 1972 and 1973 were preceded in each year by a rise in the *Trichostrongylus* spp. egg counts in the seeder lambs. Despite the fact that these egg counts remained at a fairly high level until November 1972, the infestation acquired from the pasture decreased from June onwards, when the temperature at soil level was probably unfavourable for the development of the majority of eggs and larvae (Levine & Andersen 1973). The atmospheric temperatures recorded in Fig. 2 can only serve as a rough guide as they were recorded above the ground in a sheltered locality and Andersen, Levine & Boatman (1970) have shown that these temperatures are invariably lower than those recorded at the soil surface beneath 7–10 cm of grass.

The increased worm burdens during autumn confirm the observations of other workers that the free-living stages of this genus thrive during cool, moist conditions (Muller, 1968; Donald, 1968; Anderson, 1972).

Cooperia spp.

The *Cooperia* spp. infestations in Survey 1 were acquired from the pasture on which the calves had grazed. Those present in the sheep slaughtered in September and October 1969 had probably been acquired by the lambs when they passed through the pasture grazed by the calves, on the way to their own pasture.

Oesophagostonum columbianum

The recovery of *O. columbianum* in Survey 2 after its virtual disappearance in the tracer lambs slaughtered during the latter half of Survey 1 indicates that this parasite may take a particularly long time to become established on artificial pastures. The long prepatent period of this parasite (Veglia, 1923) and relatively small numbers of adults recovered generally (Barrow, 1964; Rossiter, 1964) would contribute considerably to this phenomenon. The long prepatent period accounts for the virtual absence of *O. columbianum* in many areas where it had previously occurred, but where the simultaneous occurrence of *H. contortus* during the summer months had necessitated the use of broad-spectrum anthelmintics administered regularly at short intervals.

The peak burdens of *O. columbianum* recovered during May 1972 and 1973 could be because regrowth of the pastures had slowed down or ceased and that more larvae per unit mass of feed were thus available. This seems to apply to other genera too, but, whereas it became too cold after this for the further development of *H. contortus* or *O. columbianum* on the pastures, the nematodes, which prefer cooler conditions, were still recovered in subsequent months.

Dictyocaulus filaria

The increase of *D. filaria* infestation in the lambs slaughtered in Survey 1 during May–July 1970 may be due to 2 factors. Firstly, the cooler conditions were favourable for the free-living stages (Rose, 1955) and, secondly, the introduction of the 18 worm-free Merino and 14 worm-free Karakul lambs during March and May resulted in increased pasture contamination. The flock lambs would by this time be reasonably resistant to *D. filaria* infestation and thus pasture contamination would be low. The introduction of this large number of susceptible lambs would boost pasture contamination once they became infested and result in increased burdens in the tracer lambs. During July 1970, 2 of the Karakul lambs succumbed to massive *D. filaria* infestations, thus indicating that infestation continued to increase during the winter months.

No attempt was made to recover the larval stages of *D. filaria* from the lymph glands of the tracer lambs as described by Anderson & Verster (1971). It is probable that the total recorded worm burdens of this species would have been higher had this been done.

No lungworms were recovered from any of the sheep slaughtered in Survey 2, the result probably of the removal of all the susceptible sheep from the pasture during the months between the 2 surveys. The remaining seeder sheep, had probably acquired a solid immunity because of the prolonged exposure to infestation and were thus incapable of re-contaminating the pastures.

Moniezia expansa

The seasonal incidence of this cestode is largely dependent on the oribatid mites which serve as intermediate hosts. The fact that the development of the cysticercoids to maturity in the mites is retarded during the winter months (Kuznetsov, 1970), accounts for the lower seasonal incidence of infestation during these months. Large numbers of these overwintering cysticercoids will mature during spring and thus account for the high burdens in the lambs slaughtered during November (Table 3). In the United States, Worley, Jacobson & Barrett (1974) have suggested that the high incidence of cestode infestation in lambs grazed for a limited period on summer pastures is due to their ingestion of overwintering oribatid mites containing tapeworm cysticercoids.

During December and January the length of the days and the atmospheric temperatures both increase and the mites are probably only available on the pasture from the late afternoon until the early morning (Soulsby, 1965). As the sheep in these surveys were generally housed during these times this could account for the decrease in incidence during these months. With the advent of cooler weather and shorter days during February and the remaining summer and autumn months, the incidence of infestation increased again.

General

With slight species variations, lower levels of infestation of most nematode species were encountered in the tracer lambs slaughtered from September–December. In Victoria, Australia, Anderson (1972) considered it significant that larvae tended to disappear rapidly from the pasture when the mean temperature rose above 15 °C after a period of colder weather, and at the same time relative humidity was also decreasing. Southcott *et al.* (1976) suggest that climatological stresses appear to be the most likely factors involved in larval disappearance. At Hennops River, solar irradiation must be considered as a stress factor during these months as pasture regrowth is only just beginning, rainfall is sparse and consequently cloud cover is poor.

ACKNOWLEDGEMENTS

The authors wish to thank Mrs S. M. Raymond and Miss I. Penderis for their able technical assistance.

REFERENCES

ANDERSEN, F. L., LEVINE, N. D. & BOATMAN, P. A., 1970. Survival of third-stage *Trichostrongylus colubriformis* larvae on pasture. *Journal of Parasitology*, 56, 209–232.

ANDERSON, N., 1972. Trichostrongylid infections of sheep in a winter rainfall region. I. Epizootiological studies in the Western District of Victoria, 1966–67. *Australian Journal of Agricultural Research*, 23, 1 113–1 129.

ANDERSON, N., 1973. Trichostrongylid infections of sheep in a winter rainfall region. II. Epizootiological studies in the Western District of Victoria, 1967–68. *Australian Journal of Agricultural Research*, 24, 599–611.

ANDERSON, P. J. S. & VERSTER, ANNA, 1971. Studies on *Dictyocaulus filaria*. I. Modifications of laboratory procedures. *Onderstepoort Journal of Veterinary Research*, 38, 181–184.

ARMOUR, J. & BRUCE, R. G., 1974. Inhibited development of *Ostertagia ostertagi* infections—a diapause phenomenon in a nematode. *Parasitology*, 69, 161–174.

BARROW, D. B., 1964. The epizootiology of nematode parasites of sheep in the Border area. *Onderstepoort Journal of Veterinary Research*, 31, 151–162.

BLITZ, N. M. & GIBBS, H. C., 1972. Studies on the arrested development of *Haemonchus contortus* in sheep. II. Termination of arrested development and the spring rise phenomenon. *International Journal for Parasitology*, 2, 13–22.

BRUNSDON, R. V., 1973. Inhibited development of *Haemonchus contortus* in naturally acquired infections in sheep. *New Zealand Veterinary Journal*, 21, 125–126.

CONNAN, R. M., 1971. The seasonal incidence of inhibition of development in *Haemonchus contortus*. *Research in Veterinary Science*, 12, 272–274.

DENHAM, D. A., 1969. The development of *Ostertagia circumcincta* in lambs. *Journal of Helminthology*, 43, 299–310.

DONALD, A. D., 1968. Ecology of the free-living stages of nematode parasites of sheep. *Australian Veterinary Journal*, 44, 139–144.

HORAK, I. G. & LOUW, J. P. Parasites of domestic and wild animals in South Africa. VI. Helminths in calves on irrigated pastures on the Transvaal Highveld. *Onderstepoort Journal of Veterinary Research*, In press.

JAMES, P. S. & JOHNSTONE, I. C., 1967. Studies with *Ostertagia circumcincta* with sheep, I. The epidemiology of mature adults and arrested larvae. *Journal of Helminthology*, 41, 137–150.

KAUZAL, G., 1933. Seasonal incidence of gastro-intestinal parasites of fat sheep in New South Wales. *Australian Veterinary Journal*, 9, 179–186.

KUZNETSOV, M. I., 1970. (Development times of *Moniezia* cysticercoids in *Scheloribates laevigatus* under natural conditions). *In* (Oribatids and their role in the processes of soil formation) (Ed. by E. M. Bulanova-Zakhvatkina *et al.*) (In Russian) Vilnius: Akademiya Nauk Litovskoi SSR pp 223–227. (Abstract in *Helminthological Abstracts*, Series A, 40, 448, 1971).

LEVINE, N. D. & ANDERSEN, F. L., 1973. Development and survival of *Trichostrongylus colubriformis* on pasture. *Journal of Parasitology*, 59, 147–165.

MICHEL, J. F., 1974. Arrested development of nematodes and some related phenomena. *Advances in Parasitology*, 12, 279–366.

MULLER, G. L., 1968. The epizootiology of helminth infestation in sheep in the South-Western districts of the Cape. *Onderstepoort Journal of Veterinary Research*, 35, 159–194.

REID, J. F. S. & ARMOUR, J., 1972. Seasonal fluctuations and inhibited development of gastro-intestinal nematodes of sheep. *Research in Veterinary Science*, 13, 225–229.

REINECKE, R. K., 1967. Improved methods for the recovery of parasitic nematodes at autopsy. *Onderstepoort Journal of Veterinary Research*, 34, 547–562.

ROSE, J. H., 1955. Observations on the bionomics of the free-living larvae of the lungworm *Dictyocaulus filaria*. *Journal of Comparative Pathology and Therapeutics*, 65, 370–381.

ROSSITER, L. W., 1964. The epizootiology of nematode parasites of sheep in the coastal area of the Eastern Province. *Onderstepoort Journal of Veterinary Research*, 31, 143–150.

SHONE, D. K. & PHILIP, J. R., 1967. Anthelmintic and toxicity studies with tetramisole. I. Anthelmintic efficacy. *Journal of the South African Veterinary Medical Association*, 38, 165–176.

SNIJDERS, A. J., STAPELBERG, J. H. & MULLER, G. L., 1971. Low level thiabendazole administration to sheep. I. Susceptibility of medicated sheep to natural infestations at Outeniqua. *Journal of the South African Veterinary Medical Association*, 42, 155–167.

SOULSBY, E. J. L., 1965. Textbook of Veterinary Clinical Parasitology, Volume I. Helminths. Oxford, Blackwell Scientific Publications.

SOUTHCOTT, W. H., MAJOR, G. W. & BARGER, I. A., 1976. Seasonal pasture contamination and availability of nematodes for grazing sheep. *Australian Journal of Agricultural Research*, 27, 277–286.

VEGLIA, F., 1915. The anatomy and life-history of the *Haemonchus contortus* (Rud). *Report of the Director of Veterinary Research, Union of South Africa*, 3/4, 347–500.

VEGLIA, F., 1923. Preliminary notes on the life-history of *Oesophagostomum columbianum*. *Report of the Director of Veterinary Research, Union of South Africa*, 9/10, 809–829.

VILJOEN, J. H., 1964. The epizootiology of nematode parasites of sheep in the Karoo. *Onderstepoort Journal of Veterinary Research*, 31, 133–142.

VILJOEN, J. H., 1969. Further studies on the epizootiology of nematode parasites of sheep in the Karoo. *Onderstepoort Journal of Veterinary Research*, 36, 233–264.

WALLER, P. J. & THOMAS, R. J., 1975. Field studies on inhibition of *Haemonchus contortus* in sheep. *Parasitology*, 71, 285–291.

WORLEY, D. E., JACOBSON, R. H. & BARRETT, R. E., 1974. The chronology of tapeworm (*Moniezia expansa*) acquisition by sheep on summer ranges in Montana and Idaho. *Proceedings of the Helminthological Society of Washington*, 41, 19–22.

Printed by and obtainable from The Government Printer, Private Bag X85, Pretoria, 0001