# THE INCIDENCE OF HELMINTHS IN PIGS, SHEEP, CATTLE, IMPALA AND BLESBOK IN THE TRANSVAAL

by

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*To Valerie, Howard and Anthonie*

# DECLARATION

During the surveys conducted in sheep and cattle at Hennops River, Mr. J.P. Louw counted and identified many of the worms and is co-author of the two articles that have appeared on this aspect of the research. Mrs. S.M. Raymond and Miss I. Penderis assisted in the recovery and counting of helminths in these surveys and those conducted in pigs and with the processing of the necropsies of the blesbok from Lunsklip. The cattle and impala from Boekenhout were processed for worm recovery with the help of Miss C. Brückner, Miss E. Jansen van Vuuren and Mr. I.L. de Villiers, and the impala from Pafuri and blesbok from Badplaas with that of Mrs. M.R. Brown.

With the exception of the abovementioned assistance this thesis is the candidate's own original work. It has not been previously submitted and is not concurrently being submitted in candidature for any other degree.

Candidate ..................

I.G. Horak

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# ABSTRACT

The seasonal incidence of helminth infestation in pigs, sheep, cattle, impala and blesbok was determined from fluctuations in the worm burdens of these animals exposed to natural infestation at particular localities in the Transvaal and culled at various, fairly regular intervals. The prevalence of infestation in pigs slaughtered at the Pretoria Municipal Abattoir and in impala near Pafuri and blesbok at Badplaas was also established.

## *Pigs*

Seventy-three percent of pigs marketed at the Pretoria Municipal Abattoir by farmers were infested with helminths and *Ascarops strongylina*, *Ascaris suum* and *Oesophagostomum* spp. were the most prevalent. All the pigs marketed by speculators were infested, and *Ascarops strongylina* and *Physocephalus sexalatus* were the helminths most frequently recovered.

In pigs kept under semi-intensive conditions at Boekenhoutkloof, *Ascarops strongylina* and *Trichuris suis* were recovered in the largest numbers from November to March. Although many pigs were infested with *Ascaris suum* no seasonal pattern could be determined.

## *Sheep*

The greatest worm burdens of *Haemonchus contortus* were recovered from sheep on irrigated or dry-land pasture on the Transvaal Highveld from February to April or May; *Ostertagia* spp. from April to October on irrigated pasture and during March and April on dry-land pasture; *Trichostrongylus* spp. from March or April to June and *Moniezia expansa* from November to April or May. The development of *Haemonchus contortus* was arrested in the fourth larval stage from April or May to June or August and *Ostertagia* spp. from June or July to August.

## *Cattle*

Large numbers of *Haemonchus placei* were recovered during June and July from calves on irrigated pasture at Hennops River. Marked arrest in larval development was evident from May to November. *Trichostrongylus* spp. were generally recovered in the largest numbers during May, June and October and *Cooperia* spp. from March to June.

On natural pasture near Boekenhout peak burdens of *Haemonchus placei* were recovered from cattle during December and January and marked arrest in development was present from April to July. The largest numbers of *Trichostrongylus* spp. were recovered during December; *Cooperia* spp. from April to June and during December and *Oesophago=stomum radiatum* from June to January.

*Impala (Aepyceros melampus)*

Peak burdens of adult *Haemonchus placei, Longistrongylus sabie, Impalaia tuberculata, Cooperia hungi* and *Cooperioides hamiltoni* were generally present in impala culled near Boekenhout from November to February. The development of these nematodes was arrested during the fourth larval stage from April or June to September or October.

Sheep and goats were successfully artificially infested with infective larvae of the helminths listed in the previous paragraph and those of *Trichostrongylus colubriformis, Trichostrongylus falculatus* and *Oesophagostomum columbianum* cultured from impala faeces. Calves were also successfully infested with these worms but *Cooperioides hamiltoni* and *Oesophagostomum columbianum* did not become established.

Twelve impala shot near Pafuri during August 1977 were infested with 13 species of helminths. The most abundant species recovered were *Trichostrongylus colubriformis, Cooperia connochaeti, C. hungi, Cooperioides hamiltoni, Impalaia tuberculata* and *Strongyloides papillosus.*

*Blesbok (Damaliscus dorcas phillipsi)*

Peak numbers of *Haemonchus contortus* were recovered from blesbok at Lunsklip from August to March and *Impalaia nudicollis* from January to April and during September. Sheep were successfully artificially infested with infective larvae of *Haemonchus contortus, Trichostrongylus axei, T. falculatus* and *Impalaia nudicollis* cultured from blesbok faeces.

Twenty-eight blesbok, culled at Badplaas from May to July 1978 harboured 17 helminth species. Of these *Haemonchus* spp., *Longistrongylus albifrontis, Trichostrongylus thomasi, Cooperia hungi, Cooperia yoshidai* and *Impalaia tuberculata* were the most abundant.

The following helminths, recovered from naturally infested animals in the various surveys, are new records: *Impalaia tuberculata* and *Longistrongylus sabie* for cattle; *Bunostomum trigonocephalum, Gongylonema pulchrum, Haemonchus placei, Trichostrongylus falculatus* and *Fasciola gigantica* for impala and *Cooperia hungi, Haemonchus bedfordi, Trichostrongylus thomasi* and *Skrjabinema alata* for blesbok.

Survey methods, host specificity, geographical distribution of helminth parasites, the seasonal incidence of the major nematode genera, arrested development and control measures are discussed.

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# GENERAL INTRODUCTION

It has been estimated that helminth infestation in domestic livestock costs the South African agricultural industry between R80 and R100 million annually (Kotze and Thompson: Personal communications). It is difficult to estimate the effect of infestation on the productivity of free-ranging antelope but even moderate confinement may result in helminthosis and mortality (Van der Walt & Ortlepp, 1960).

The most important meat-producing domesticated mammals in the Republic of South Africa (RSA) are cattle, sheep and pigs, while sheep also produce wool. Impala *(Aepyceros melampus)* and blesbok *(Damaliscus dorcas phillipsi)* are amongst the antelope species most frequently cropped for meat. Because of their considerable contribution to the economy the domestic animals mentioned above were selected for survey purposes, while animals of the two antelope species were placed at my disposal by the Division of Nature Conservation of the Transvaal Provincial Administration and the National Parks Board.

Although the epizootiology of many nematode parasites of sheep,based on worm counts at necropsy, has been determined in the Cape Province (Barrow, 1964; Rossiter, 1964; Viljoen, 1964, 1969; Muller, 1968) no such studies have been conducted in the Transvaal. Nor has the seasonal incidence of helminth infestation in pigs, cattle, impala and blesbok, based on worm counts, been determined in the RSA.

Much of this thesis is based on results of helminth surveys conducted by Horak (1978a, b, c, d, e, f) and Horak & Louw (1977, 1978) in pigs, sheep, cattle, impala and blesbok, and it is divided into two parts, the first dealing with helminths of pigs and the second with those of ruminants. The prevalence of helminths in swine was determined either by examining pigs slaughtered at the Pretoria Municipal Abattoir for a period of one year, or by examining tracer pigs kept under semi-intensive conditions of management in order to determine the seasonal incidence of infestation. To ascertain seasonal fluctuations of helminth infestation in sheep, cattle, impala and blesbok these animals, exposed to natural infestation in particular localities, were culled at various intervals over periods varying from 12 to 26 months and their worms counted.

In addition the incidence of infestation in 12 impala culled during the course of a single week and 28 blesbok culled during three consecutive months was determined.

Antelope are frequently kept on the same pastures as domestic livestock and cross-infestation with helminths may occur (Mönnig, 1931a, 1932, 1933; Hammond, 1972; Prestwood, Kellogg, Pursglove & Hayes, 1975; Prestwood, Pursglove & Hayes, 1976). This possibility was examined in the present study by artificially transmitting nematodes from blesbok to sheep and from impala to sheep, goats and cattle.

The results of the surveys and cross-transmission experiments are discussed in the light of their contribution to the understanding of the epizootiology of parasitic infestation and of the geographical distribution of parasites and their host preferences. Measures to control helminth infestation in livestock and antelope in the Transvaal are suggested.

## GENERAL MATERIALS AND METHODS

### *Surveys and survey animals*

Two surveys were conducted in pigs. In the one, 94 pigs of various breeds and ages were slaughtered at the Pretoria Municipal Abattoir and examined for helminth infestation. In the other, 38 newly weaned Large White pigs run on a commercial pig farm were slaughtered and examined.

Three surveys were conducted in lambs. A total of 168 four to ten-month-old lambs of which the majority were Merinos and the remainder Dormers were slaughtered in these surveys. In the two surveys conducted in cattle 26 five-month-old Friesland-type calves were examined in the one and 23 12 to 18-month-old Africander-type cattle in the other.

The two antelope species surveyed were impala and blesbok. Forty-eight animals of the former species were examined in two separate surveys and 60 of the latter also in two separate surveys.

*Study Areas*

The study areas or nearest reference points to these areas are indicated in Fig. 1.

The region covered by the survey in pigs slaughtered at the Pretoria Municipal Abattoir includes virtually the whole of the Transvaal and part of the northern Orange Free State because this is the area from which pigs are consigned to this abattoir. This is a summer rainfall region with dry winters.

The survey in Large White pigs was conducted on a pig and poultry farm in the Boekenhoutkloof area ($25^{o}42$'S; $28^{o}03$'E; Alt. $\pm$ 1341m) which lies in the Magaliesberg range to the west of Pretoria. The pigs were kept in an earthern floored pen 200$m^2$ in extent which was reduced to 100$m^2$ during the survey.

In two of the surveys sheep grazed either 2,5 or 1,2 ha of sprinkler irrigated pasture at Hennops River ($25^{o}50$'S; $27^{o}58$'E; Alt. $\pm$ 1280m) approximately 15 km west of Pretoria. Although this region is classified as Bankenveld by Acocks (1975), the pastures consisted of an artificially established mixture of grasses and clovers. The other survey in sheep was conducted on artificially established and natural dry-land grass pastures on a farm near Tonteldoos ($25^{o}19$'S; $29^{o}59$'E; Alt. 1676m) in the Dullstroom district of the Transvaal, classified as North-Eastern Sandy Highveld by Acocks (1975).

Approximately 1,0ha of sprinkler irrigated, artificially established grass and grass/clover pasture at Hennops River was used for the survey in Friesland-type calves. A 750ha area of Mixed Bushveld (Acocks, 1975) in the Nylsvley Provincial Nature Reserve ($24^{o}29$'S; $28^{o}42$'E; Alt. $\pm$ 1110m) near Boekenhout in the northern Transvaal was used in the seasonal incidence surveys conducted in Africander-type cattle and impala. The vegetation in this area consisted of trees, among which *Burkea africana* predominated, shrubs, chiefly *Ochna pulchra* and *Grewia flavescens*, and a herbaceous layer consisting mainly of the grasses *Eragrostis pallens* and *Digitaria eranthia* (Hirst, 1975).

A Sour Bushveld camp (Acocks, 1975), which was increased from 1630ha to 2060ha during the survey, in the Percy Fyfe Provincial Nature

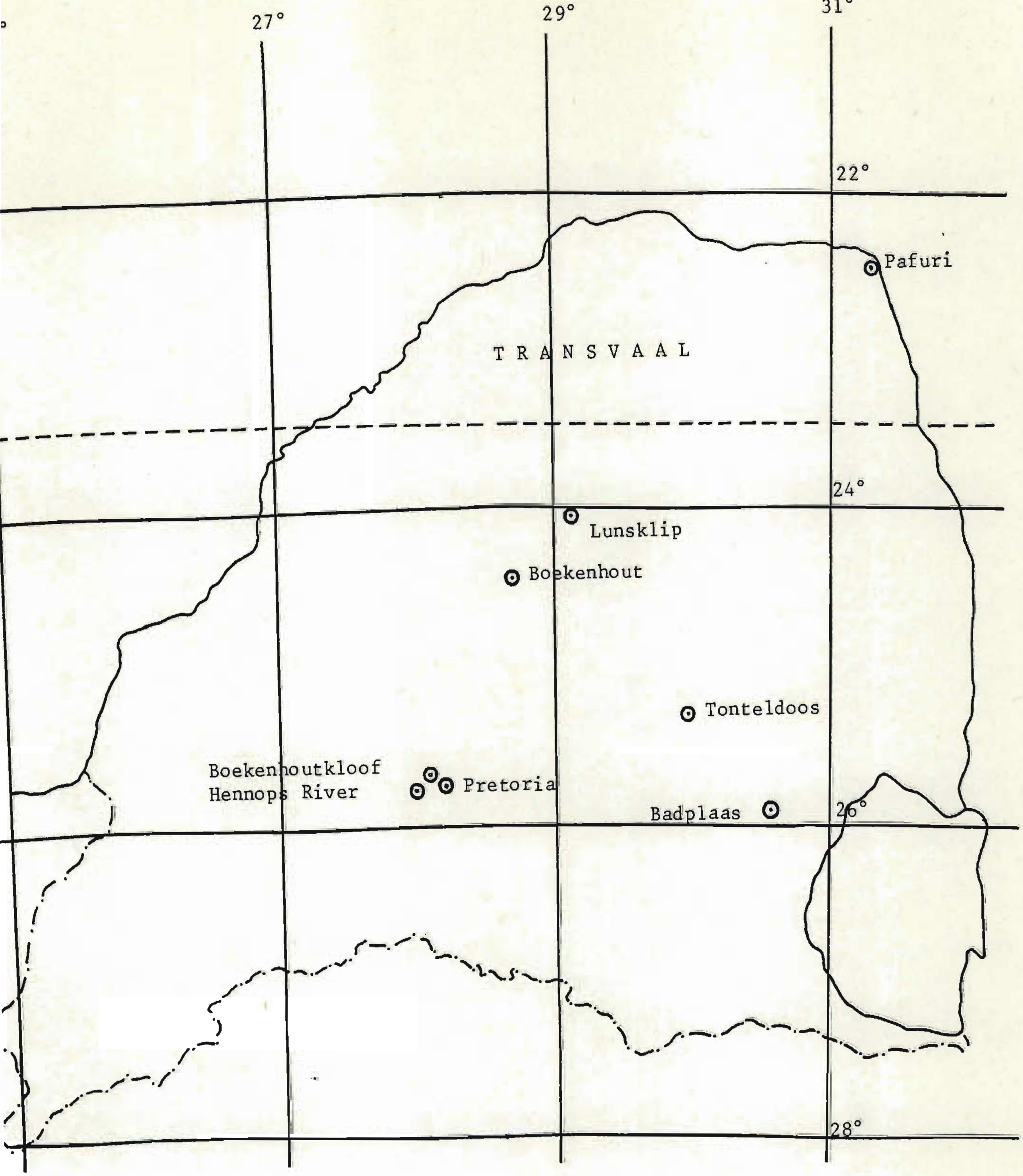



Fig. 1 The localities at which helminth surveys were conducted in the Transvaal, RSA

Reserve situated at Lunsklip (24°01'S; 29°07'E; Alt. 1475m) in the northern Transvaal served as study area for the seasonal incidence survey in blesbok.

In further helminth prevalence surveys in antelope 12 impala were shot in the Pafuri area (22°27'S; 31°18'E; Alt. ± 305m) of the Kruger National Park. This is a Mixed Bushveld region (Acocks, 1975) and is situated on the north-eastern border of the Transvaal, and 28 blesbok were culled in the Rob Ferreira Provincial Nature Reserve at Badplaas (25°57'S; 30°34'E; Alt. ± 1067m). This reserve is approximately 400ha in extent and situated in a region classified as Piet Retief Sourveld by Acocks (1975).

The geographical coordinates of the nearest reference point as listed in the Official Standard Names Gazetteer, Union of South Africa (United States Board on Geographical Names, 1954) are given where those of the actual study area are not known. These reference points rather than the actual localities of the surveys are used to identify the locality of each of the surveys.

*Climatological and other data*

Daily minimum and maximum atmospheric temperatures and rainfall were recorded at some survey sites, or were obtained from weather stations in the vicinity. When irrigation was applied the approximate amount of water supplied at each occasion was noted.

*Tracer animals*

Tracer animals were used in the seasonal incidence surveys conducted in pigs, sheep and cattle. With the exception of the Africander cattle at Boekenhout, these were animals raised and maintained under worm-free conditions. All the sheep and cattle were in addition treated with large doses of broad-spectrum anthelmintics immediately prior to their exposure to infestation in the survey areas in order to rid them of nematode infestations they might have previously acquired.

The cattle near Boekenhout had grazed on natural pastures from birth and were treated with three times the therapeutic dose of a broad-spectrum anthelmintic on the day that their particular terms as tracers commenced.

The tracers were exposed in the survey areas in groups of two to four and were slaughtered after predetermined periods. In two surveys consecutive groups of tracers overlapped by a month, in others by a few days while in others the next group of tracers was introduced on the day the previous group was removed. These animals were starved for 24 to 48h prior to necropsy.

*Helminth recovery*

The gastro-intestinal ingesta of the pigs and sheep and of the calves at Hennops River were processed in a modified Baermann apparatus incubated at 42°C in a waterbath as described by Shone & Philip (1967) and Reinecke (1967, 1972). The filtrates were washed over sieves with 38 μm apertures and residues over sieves with 150 μm apertures. Representative samples amounting to 1/5 of the abomasal and small intestinal ingesta of the cattle from Boekenhout were washed over sieves with 38 μm apertures, and 2/5 of the large intestinal ingesta of these animals were washed over sieves with 150 μm apertures. The remainder of the ingesta was discarded.

The entire abomasal and small intestinal contents of the impala and of blesbok at Badplaas were sieved on sieves with 38 μm apertures and those of the large intestines on sieves with 150 μm apertures.

In order to recover larval stages from the ingesta of the blesbok at Lunsklip 1/10 aliquots were taken of the contents of the abomasum, small intestine and large intestine and sieved on sieves with 38 μm apertures. The other 9/10 of the ingesta of these organs were sieved on coarser sieves (150 μm apertures).

The livers, or portions thereof, of all animals were sliced and incubated for 2½ to 4h in an 0,9 % solution of NaCl in a modified Baermann apparatus or in large flasks in a waterbath maintained at approximately 42°C. After removal of the liver slices the saline solution was washed over sieves with 38 μm apertures.

The tracheae and bronchial trees of both lungs of the pigs, sheep, impala and blesbok and tracheae and right lungs only of cattle were opened and thoroughly washed and the washings sieved over sieves with 38 μm apertures. With the exception of those of the cattle at Boekenhout, and all the impala and the blesbok at Badplaas, the lungs were then cut into cubes and incubated in a 1,2 % saline solution in a waterbath at 42°C for 2½ to 4h using a modification of the technique described by Anderson & Verster (1971). After removal of the lung cubes the salt solution was sieved over sieves with 38 µm apertures.

The mucosae and muscularis layers of the abomasa, small intestines and large intestines were stripped by scraping the gut wall with glass slides and the scrapings subjected to pepsin/HCl digestion as described by Herlich (1956) and modified by Reinecke (1972). The mucosae of the stomachs of some pigs were digested while those of others were added to the stomach ingesta in the waterbath. Portions of livers of some pigs at Boekenhoutkloof were also digested in a pepsin/HCl solution. All the digested material was sieved over sieves with 38 µm apertures. No digests of the gut wall were done in the impala from Pafuri.

The particles of ingesta and digests which remained on the sieves were preserved by adding approximately 1/10 by volume of a 10 % formaldehyde solution, and stored for future examination.

*Helminth identification*

The descriptions used for the identification of adult helminths of the various genera and their parasitic larval stages are listed in Tables 1 and 2.

Although most of the adult worms and some of the parasitic, immature stages of these worms have been adequately described by the authors listed in Tables 1 and 2, the identification of some adult worms still presents problems and many immature worms have as yet not been described. The difficulties encountered in identifying these worms are worth listing:-

*Ascarops* and *Physocephalus*: Third stage infective larvae, recovered from their beetle intermediate hosts, have been described by Alicata (1935). I have, however, been unable to find a description of the immature parasitic stages. Alicata (1935) described a short buccal cavity, longer pre-oesophagus and smooth, knoblike process on the tip of the tail for the third stage larvae of *Ascarops strongylina,* while the larvae of *Physocephalus sexalatus* have a long buccal cavity, shorter

TABLE 1 The descriptions used for the identification of helminths recovered from pigs, sheep, cattle, impala and blesbok in the Transvaal

| Genus | Description |
|---|---|
| *Agriostomum* | Mönnig (1929) |
| *Ascaris* | Soulsby (1968) |
| *Ascarops* | Mönnig (1934) |
| *Bunostomum* | Ransom (1911a) |
| *Capillaria* | Ransom (1911a) |
| *Chabertia* | Ransom (1911a) |
| *Cooperia* | Ransom (1911a), Mönnig (1931a, 1939), Boomker, Horak & Alves (1979) |
| *Cooperioides* | Mönnig (1933), Ortlepp (1938) |
| *Dictyocaulus* | Mönnig (1932, 1934) |
| *Gongylonema* | Skrjabin, Sobolev & Ivashkin (1967) |
| *Haemonchus* | Ransom (1911a), Roberts, Turner & McKevett (1954), Sachs, Gibbons & Lweno (1973), Gibbons (1979) |
| *Impalaia* | Mönnig (1924, 1931a), Gibbons, Durette-Desset & Daynes (1977), Boomker (1977) |
| *Longistrongylus* | Mönnig (1933), Gibbons (1977) |
| *Metastrongylus* | Mönnig (1934) |
| *Nematodirus* | Becklund & Walker (1967) |
| *Oesophagostomum* | Ransom (1911a), Goodey (1924, 1925) |
| *Ostertagia* | Ransom (1911a) |
| *Physocephalus* | Mönnig (1934) |
| *Skrjabinema* | Mönnig (1932) |
| *Strongyloides* | Ransom (1911a) |
| *Trichostrongylus* | Mönnig (1925, 1933, 1934), Nagaty (1932) |
| *Trichuris* | Skrjabin, Shikhobalova & Orlov (1957) |
| *Avitellina* | Mönnig (1934) |
| *Moniezia* | Mönnig (1934) |
| *Fasciola* | Mönnig (1934) |
| *Paramphistomum* | Mönnig (1934) |

TABLE 2 The descriptions used for the identification of parasitic larval stages of nematodes recovered from pigs, sheep, cattle, impala and blesbok in the Transvaal

| Genus | Description |
|---|---|
| *Ascaris* | Douvres, Tromba & Malakatis (1969) |
| *Ascarops* | Alicata (1935) |
| *Cooperia* | Douvres (1957b) |
| *Haemonchus* | Veglia (1915) |
| *Nematodirus* | Kates & Turner (1955) |
| *Oesophagostomum* | Veglia (1923), Douvres (1957b) |
| *Ostertagia* | Douvres (1956) |
| *Physocephalus* | Alicata (1935) |
| *Trichostrongylus* | Mönnig (1926), Douvres (1957a) |

pre-oesophagus and digitiform, knoblike process on the tip of their tails. These characteristics persisted in the immature parasitic stages and were used to identify the larvae generically.

*Cooperia* and *Cooperioides*: The fourth stage larvae of *Cooperia* have been described by Douvres (1957b), but there is no description of these larvae for *Cooperioides*. Because of quite marked similarities between the adult worms of these genera {Mönnig (1933) originally described *Cooperioides hamiltoni* as *Cooperia hamiltoni*}, I have assumed that the larval stages would also be similar and hence not readily distinguishable. This assumption may, however, not be valid.

*Cooperia connochaeti*: This is a new species and has been described from blue wildebeest and impala (Boomker, Horak & Alves, 1979).

*Haemonchus* spp.: The differences in morphology between both the third stage infective larvae and the adults of *Haemonchus contortus* and *Haemonchus placei* have been described by Roberts, Turner & McKevett (1954). These differences are almost entirely based on the greater lengths and breadths of certain structures in *H. placei* than *H. contortus*. It is impossible to utilize these criteria to distinguish the fourth stage larvae of these species from one another as larvae of all ages and sizes in this particular stage of development may be present and comparisons based on length and breadth are thus impractical.

In a revision of the genus *Haemonchus*, Gibbons (1979) does not accept *H. placei* as a valid species because it cannot be differentiated from *H. contortus* on the basis of reliable morphological characters. She states "morphological differences reported between the two species, such as measurements, are not dicisive and overlap and, in any case, are also related to host differences." Furthermore "there is no reason to accept that the biological differences between *H. placei* and *H. contortus* are other than those between strains of the same species." She argues that all other species of *Haemonchus* can be distinguished by clear morphological differences in the male and concludes that *H. placei* is to be regarded as a synonym of *H. contortus*.

I do not feel that the arguements proffered by Gibbons (1979) in her discussion are sufficient to negate the validity of the morphological and particularly biological differences between these two species, as will become evident later in this thesis, and I have retained *H. placei* as a valid species.

The immature parasitic stages of *Haemonchus bedfordi* have as yet not been described. I have assumed that they would be similar to, and hence not easily distinguishable from those of *H. contortus* or *H. placei*.

*Impalaia* spp.: Mönnig (1931a) described the third stage infective larvae of *Impalaia nudicollis*, within the sheath of the second stage, as having a tail that ends in two distinct points as though a wedge-shaped piece had been cut from it. Third stage infective larvae of *Impalaia tuberculata* cultured from the faeces of infested impala culled during the present surveys appeared to be identical to those of *I. nudicollis*.

The cuticle around the anterior extremity of worms of this genus is slightly inflated, similar to that of *Cooperia* spp., and fourth stage larvae with inflated cephalic extremities could thus belong to *Cooperia* spp., as described by Douvres (1957b), or to *Impalaia* spp. But whereas *Cooperia* spp. larvae have tails ending in a single point, larvae with tails with two distinct points were also recovered and these were assigned to whichever species of adult *Impalaia* was present in the same host, as mixed infestations with adults of *I. nudicollis* and *I. tuberculata* were not encountered.

The genus *Impalaia* has recently been reviewed by Gibbons, Durette-Desse & Daynes (1977) and Boomker (1977) and these authors regard *I. nudicollis* and *I. tuberculata* as valid species. Their desriptions of the dorsal bursal rays of these worms and the comparatively huge bursa of *I. tuberculata* were used to distinguish this species from *I. nudicollis*.

*Longistrongylus* spp.: Gibbons (1977) proposed that the genera *Bigalkenema* and *Kobusinema* be regarded as synonyms of the earlier genus *Longistrongylus* because of morphological similarities, and that the species of these two genera be transferred to *Longistrongylus*; con=sequently *Longistrongylus sabie* is used in this thesis instead of *Bigalkenema sabie*.

Adult *Longistrongylus albifrontis* and *L. sabie* are very similar in appearance and I found that the most reliable characters for distinguishing the males from each other were the slightly longer spicules and stouter dorsal bursal ray bifurcating in its distal third in *L. sabie*, compared with shorter spicules and a dorsal ray bifurcating halfway along its length in *L. albifrontis* as described by Gibbons (1977).

These worms are also similar in morphology to *Ostertagia* spp. and I have assumed that their larval stages would also resemble those of *Ostertagia* spp. Consequently the description by Douvres (1956) of the fourth stage larvae of *Ostertagia ostertagi* was used to identify the larvae of *Longistrongylus* spp. and differentiate them from other larvae present in the abomasa. None of the animals examined harboured adult *L. albifrontis* and *L. sabie* at the same time or either of these worms and adult *Ostertagia* spp. simultaneously. Therefore any fourth stage larvae recovered resembling *O. ostertagi* were assigned to the species of the adult worm present in that particular host.

*Skrjabinema alata*: The description of this species by Mönnig (1932) was based on seven female worms recovered from the colon of a sheep. These worms had apparently been sent by a farmer or veterinarian to the Veterinary Research Institute, Onderstepoort. The female worms of this genus recovered from blesbok in these surveys conform to the description of *S. alata* and associated males, which have not yet been described, were assumed to belong to the same species.

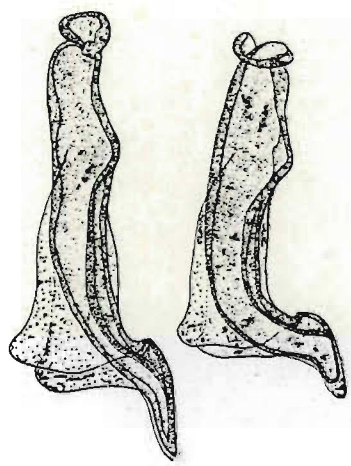
*Trichostrongylus* spp.: Only the adult male worms of this genus can be identified with any certainty. Consequently, whenever a number of *Trichostrongylus* species were recovered from a single host all the adult worms were counted and the males specifically identified. The females were assigned to the various species in the same proportions that the males contributed to the total *Trichostrongylus* population.

*Trichostrongylus instabilis*: The similarities between this species and *Trichostrongylus colubriformis* have been discussed by Ransom (1911a), and on the grounds of these similarities Lane (1913) made this species a synonym of *T. colubriformis*. Mönnig (1931a), apparently unaware of this change, retained the name *T. instabilis* and mentioned the variations that may occur in the spicules of the males within the species. The spicules vary in length from 0,125 mm to 0,158 mm and the chief differences are that the terminal hook may vary from between one quarter to one eighth of the total length of the spicule and the depth of the concavity of the spicule anterior to this hook may vary considerably. Subsequently Mönnig (1933), still retaining the name *T. instabilis*, illustrated what he considered to be a normal spicule, which appears to be identical to those of *T. colubriformis*, as well as an extreme variation which has a short hook and is markedly concave. If Mönnig (1931a, 1933) was correct in assigning worms with these variations in the spicule to *T. instabilis* then the synonomy of this species with *T. colubriformis* implies that the latter species contains worms with marked spicule variations. In this thesis males with these spicule variations have been assigned to *T. colubriformis*. The two types of spicules are illustrated in Fig. 2.

The spicules of so-called *T. colubriformis* recovered from cattle and impala at Boekenhout and impala at Pafuri, however, all resembled the extreme variation of *T. instabilis* as illustrated by Mönnig (1933). Moreover they retained this shape after artificial infestation of sheep, goats and calves with infective larvae harvested from cultures made from impala faeces. This prompts the suggestion that this is a valid separate species yet to be named.

*Trichostrongylus falculatus*: The spicules of males of this species have a characteristic shape, and Ransom (1911b) in his description of the species stated that the spicules measured 0,100 mm and were similar to each other in shape and size. Nagaty (1932) has shown that this is incorrect for not only do the shapes of the spicules differ slightly but the left spicule measures 0,136 mm in length and the right one only 0,127 mm.

Cestodes: The appearance of gravid segments and eggs and the width of the scolices were used for identification purposes. Gravid worms of the genera *Moniezia* and *Stilesia* were identified to species level while those considered to belong to the genus *Avitellina* were only identified to the generic level. No specific identification was attempted on non-gravid worms and these were assigned, on scolex width, to whichever adult species were present.



(a) (b)

Fig. 2 *Trichostrongylus colubriformis*. Lateral view of right spicules (after Mönnig, 1933). (a) Normal (b) Variation observed in cattle and impala in the Transvaal

### *Worm counts*

Adult *Ascaris suum*, *Haemonchus* spp., *Oesophagostomum* spp., *Paramphistomum* spp. and cestodes (scolices only) were usually counted macroscopically. Other adult nematodes and the parasitic larval stages of all species were counted with the aid of a stereoscopic microscope. Whenever present 30 to 200 adult worms and larval stages were identified microscopically using either a stereoscopic or standard microscope to determine their proportional prevalence in each population.

### *Faecal worm egg counts*

Faecal worm egg counts were done in some of the surveys, using a modification of the method of Gordon & Whitlock (1939) as described by Reinecke (1961). These counts were expressed as eggs per gram (e.p.g.) of faeces.

Wherever possible 100 infective larvae cultured from faeces were identified using the descriptions of Mönnig (1931a,b), Gordon (1933), Keith (1953) and Muller (1959). The infective larvae of *Cooperioides* spp. have not yet been described, but as adult worms of this genus and adult *Cooperia* spp. are similar in appearance it was assumed that their larvae would also be similar and hence not easily distinguishable. These larval identifications were used to determine differential faecal worm egg counts as described by Reinecke (1961), or to estimate the numbers of infective larvae of the different genera dosed to sheep, goats and cattle in the cross-transmission experiments.

## HELMINTHS RECOVERED

The helminths recovered in the various surveys and hosts from which they were recovered are summarized in Table 3.

A total of 22 nematode genera, three cestode genera and two trematode genera was recovered and 46 separate species were identified.

TABLE 3 The helminth species and hosts from which they were recovered during various surveys in pigs, sheep, cattle, impala and blesbok in the Transvaal

| Helminth species | Hosts |
|---|---|
| *Agriostomum equidentatum* Mönnig, 1929 | Blesbok |
| *Ascaris suum* Goeze, 1782 | Pigs |
| *Ascarops strongylina* (Rudolphi, 1819) | Pigs |
| *Bunostomum phlebotomum* (Railliet, 1900) | Cattle |
| *Bunostomum trigonocephalum* (Rudolphi, 1808) | Impala |
| *Capillaria* sp. | Pigs |
| *Chabertia ovina* (Fabricius, 1788) | Sheep |
| *Cooperia connochaeti* Boomker, Horak & Alves, 1979 | Impala |
| *Cooperia hungi* Mönnig, 1931 | Impala, blesbok |
| *Cooperia pectinata* Ransom, 1907 | Sheep, cattle |
| *Cooperia punctata* (von Linstow, 1906) | Sheep, cattle |
| *Cooperia yoshidai* Mönnig, 1939 | Blesbok |
| *Cooperioides hamiltoni* (Mönnig, 1932) | Impala |
| *Cooperioides hepaticae* Ortlepp, 1938 | Impala |
| *Dictyocaulus filaria* (Rudolphi, 1809) | Sheep |
| *Dictyocaulus magnus* (Mönnig, 1932) | Blesbok |
| *Gongylonema pulchrum* Molin, 1857 | Impala |
| *Gongylonema* sp. | Blesbok |
| *Haemonchus bedfordi* le Roux, 1929 | Blesbok |
| *Haemonchus contortus* (Rudolphi, 1803) | Sheep, blesbok |
| *Haemonchus placei* (Place, 1893) | Cattle, impala |
| *Impalaia nudicollis* Mönnig, 1931 | Blesbok |
| *Impalaia tuberculata* Mönnig, 1923 | Cattle, impala, blesbok |
| *Longistrongylus albifrontis* (Mönnig, 1931) | Blesbok |
| *Longistrongylus sabie* (Mönnig, 1932) | Cattle, impala |
| *Metastrongylus apri* (Gmelin, 1790) | Pigs |
| *Nematodirus spathiger* (Railliet, 1876) | Sheep, cattle |
| *Oesophagostomum columbianum* (Curtice, 1890) | Sheep, impala, blesbok |
| *Oesophagostomum dentatum* (Rudolphi, 1803) | Pigs |
| *Oesophagostomum quadrispinulatum* (Marcone, 1901) | Pigs |
| *Oesophagostomum radiatum* (Rudolphi, 1803) | Cattle |

TABLE 3 (cont)

| Helminth species | Hosts |
|---|---|
| *Ostertagia circumcincta* (Stadelmann, 1894) | Sheep, cattle |
| *Ostertagia trifurcata* Ransom, 1907 | Sheep |
| *Physocephalus sexalatus* (Molin, 1860) | Pigs |
| *Skrjabinema alata* Mönnig, 1932 | Blesbok |
| *Skrjabinema* sp. | Sheep |
| *Strongyloides papillosus* (Wedl, 1856) | Sheep, impala |
| *Strongyloides* sp. | Impala |
| *Trichostrongylus axei* (Cobbold, 1879) | Sheep, cattle, impala, blesbok |
| *Trichostrongylus colubriformis* (Giles, 1892) | Pigs, sheep, cattle, impala, blesbok |
| *Trichostrongylus falculatus* Ransom, 1911 | Sheep, cattle, impala, blesbok |
| *Trichostrongylus rugatus* Mönnig, 1925 | Sheep |
| *Trichostrongylus thomasi* Mönnig, 1932 | Blesbok |
| *Trichuris globulosa* (von Linstow, 1901) | Sheep |
| *Trichuris ovis* (Abildgaard, 1795) | Sheep |
| *Trichuris suis* (Schrank, 1788) | Pigs |
| *Trichuris* spp. | Cattle, impala, blesbok |
| *Avitellina* sp. | Sheep, blesbok |
| *Moniezia benedeni* (Moniez, 1879) | Cattle, impala |
| *Moniezia expansa* (Rudolphi, 1810) | Sheep, impala |
| *Moniezia* sp. | Blesbok |
| *Stilesia hepatica* Wolffhügel, 1903 | Impala |
| *Fasciola gigantica* Cobbold, 1856 | Impala |
| *Paramphistomum* sp. | Cattle, impala |

# PART I HELMINTHS OF PIGS

## Introduction

Helminth infestations in pigs based on worm recovery at necropsy have been determined in Canada (Martin, Gibbs & Pullin, 1974), Denmark (Jacobs, 1967), Greece (Himonas & Triantaphyllou, 1972), India (Sinha, 1968a,b), Papua, New Guinea (Talbot, 1972), the Philippines (Tongson, Castillo, Arambulo & Sarmiento, 1971), the United Kingdom (Jenkins & Erasmus, 1963; Jacobs & Dunn, 1969), the United States of America (Andrews & Connelly, 1945; Goldsby & Todd, 1957; Gaafar, 1961; Bennett & Copeman, 1970; Riddle & Forrester, 1972) and Nigeria (Fabiyi, 1979). In South Africa a checklist of parasites of the domestic pig was published by Mönnig (1928), and Ortlepp (1964a) has described some of the helminths parasitic in bushpigs and warthogs, but no actual surveys have been conducted in this country.

At the Pretoria Municipal Abattoir a large number of pigs originating from virtually the entire province of the Transvaal and part of the northern Orange Free State is slaughtered daily. Of the pigs marketed by farmers, most have usually been subjected to some form of confinement during market preparation. Speculators, on the other hand, generally purchase pigs on free range and market them directly.

This readily available source of material presented the opportunity for determining the nature and incidence of helminth parasitism in pigs and Survey 1 presents the findings of a survey conducted over a period of one year at this abattoir.

The epizootiology in Europe of *Oesophagostomum* spp. and *Hyostrongylus rubidus* in pigs, based on faecal worm egg counts and cultures, has been described by Barnett (1966), Jacobs (1966), Connan (1967) and Jacobs & Dunn (1968). In the Maritime Provinces of Canada Smith (1979) has established the epizootiology of *Oesophagostomum* spp. in swine on pasture by faecal worm egg counts and slaughter. With the exception of investigations by Andrews & Connelly (1945) and Andrews, Stewart, Richardson & McCormick (1970), who examined pigs raised on pasture in Georgia, U.S.A., no surveys involving regular slaughter of pigs from a particular locality have as yet been reported.

Survey 2 describes the use of worm-free tracer pigs for determining seasonal fluctuations in parasite availability in a pen with an earth floor.

*Survey 1 The Pretoria Municipal Abattoir*

## Materials and Methods

The lungs, livers and gastro-intestinal tracts of two pigs at a time were collected from the abattoir at intervals varying from seven to 20 days from March 1968 to February 1969. During the last five months of the survey the stomachs only of an additional two to four pigs were collected on each occasion. As a rule only pigs with a live mass of less than 100 kg were considered for survey purposes because of the greater difficulty in processing organs of larger pigs for worm recovery, but when stomachs only were collected pigs with a mass of up to 220 kg were included.

The stomachs of most of the pigs were examined also for lesions of ulceration.

## Results

For comparative purposes the worm burdens of pigs marketed by farmers are tabulated separately from those marketed by speculators. Comparisons are also made between the findings of this survey and those in other countries.

The mean worm burdens of pigs marketed by farmers and by speculators are summarized in Table 4.

Eight nematodes species were recovered, *Ascarops strongylina* and *Physocephalus sexalatus* from stomachs, *Ascaris suum* and *Trichostrongylus colubriformis* from small intestines, *Oesophagostomum dentatum*, *Oesophagostomum quadrispinulatum* and *Trichuris suis* from large intestines and *Metastrongylus apri* from the lungs of one pig. The larval stages of three cestodes were also found. These were *Cysticercus cellulosae*, *Cysticercus tenuicollis* and an *Echinococcus* sp. cyst.

TABLE 4 Survey 1. The mean worm burdens of pigs slaughtered at the Pretoria Municipal Abattoir between March 1968 and February 1969

| Source | Farmers | | | Speculators | | | Farmers | | | Speculators | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| No. of pigs examined | 26 | | | 26 | | | 22 | | | 20 | | |
| Live mass | 20-100 kg | | | 30-90 kg | | | 25-220 kg | | | 30-55 kg | | |
| Organs examined | Gastro-intestinal tract | | | Gastro-intestinal tract | | | Stomach | | | Stomach | | |
| | No. infested | Worm burden | | No. infested | Worm burden | | No. infested | Worm burden | | No. infested | Worm burden | |
| | | Mean | Range | | Mean | Range | | Mean | Range | | Mean | Range |
| Helminth species | | | | | | | | | | | | |
| *Ascarops strongylina* | | | | | | | | | | | | |
| Immature worms | 5 | 6 | 0-90 | 9 | 31 | 0-475 | 2 | 1 | 0-11 | 13 | 476 | 0-5441 |
| Adults | 16 | 54 | 0-1130 | 24 | 313 | 0-2030 | 11 | 17 | 0-125 | 18 | 198 | 0-978 |
| *Physocephalus sexalatus* | | | | | | | | | | | | |
| Immature worms | 0 | 0 | 0 | 2 | 4 | 0-80 | 0 | 0 | 0 | 0 | 0 | 0 |
| Adults | 0 | 0 | 0 | 17 | 39 | 0-319 | 1 | < 1 | 0-3 | 10 | 11 | 0-71 |
| *Trichostrongylus colubriformis* | | | | | | | | | | | | |
| Adults | 4 | 2 | 0-26 | 2 | 1 | 0-20 | - | - | - | - | - | - |
| *Ascaris suum* | | | | | | | | | | | | |
| 4th stage larvae | 2 | 1 | 0-11 | 0 | 0 | 0 | - | - | - | - | - | - |
| Adults | 7 | 2 | 0-15 | 2 | < 1 | 0-3 | - | - | - | - | - | - |
| *Oesophagostomum* spp. | | | | | | | | | | | | |
| 4th stage larvae | 2 | 11 | 0-280 | 0 | 0 | 0 | - | - | - | - | - | - |
| *O. dentatum* | | | | | | | | | | | | |
| Adults | 7 | 124 | 0-1760 | 3 | 27 | 0-702 | - | - | - | - | - | - |
| *O. quadrispinulatum* | | | | | | | | | | | | |
| Adults | 2 | 69 | 0-1203 | 1 | 1 | 0-32 | - | - | - | - | - | - |
| *Trichuris suis* | | | | | | | | | | | | |
| Immature worms | 2 | < 1 | 0-2 | 0 | 0 | 0 | - | - | - | - | - | - |
| Adults | 4 | 1 | 0-15 | 3 | 1 | 0-8 | - | - | - | - | - | - |
| *Cysticercus cellulosae* | 0 | 0 | 0 | 2 | - | - | - | - | - | - | - | - |
| *Cysticercus tenuicollis* | 0 | 0 | 0 | 2 | - | - | - | - | - | - | - | - |

Third stage parasitic larvae of *Ascarops strongylina* or *Physocephalus sexalatus* were recovered from 13 pigs and are included in the immature worm burdens of these species.

The frequency of infestation and the mean worm burdens of *Trichostrongylus colubriformis, Ascaris suum, Oesophagostomum* spp. *(O. dentatum* and *O. quadrispinulatum)* and *Trichuris suis* were greater in the pigs marketed by farmers than in those marketed by speculators. The converse, however, was true for *Ascarops strongylina, Physocephalus sexalatus, Cysticercus cellulosae* and *C. tenuicollis*.

One of the pigs marketed by a farmer harboured 244 adult *Metastrongylus apri*. This pig originated from a farm in the Belfast district of the eastern Transvaal Highveld. All other pigs marketed by farmers were consigned from farms in the Pretoria district or in the northern Transvaal.

One of the pigs marketed by a speculator was infested with *Cysticercus cellulosae* and also harboured an *Echinococcus* sp. cyst. It was impossible to trace the districts from which speculators bought their pigs because they refused to divulge this information.

Six of 36 stomachs of pigs marketed by farmers, examined for ulceration, were found to be affected, while 19 of 46 stomachs of pigs marketed by speculators had lesions.

The results of this survey and those in other countries are compared and summarized in Table 5.

The overall incidence of infestation in pigs of farm origin was lower than that recorded in other surveys, while the 100 % infestation of pigs from speculators compares with that of some surveys conducted in the United States of America.

The incidence of *Ascaris suum, Oesophagostomum* spp. and *Trichuris suis* infestation was generally lower than that encountered elsewhere, particularly in the pigs marketed by speculators. These pigs, however, had a higher incidence of *Ascarops strongylina* and *Physocephalus sexalatus* than that recorded in any other survey. Infestations with *Globocephalus* spp., *Hyostrongylus rubidus, Macracanthorhynchus hirudinaceus* or *Strongyloides ransomi* were not present in pigs examined

TABLE 5 Survey 1. The Percentage of pigs infested with helminths as determined from surveys in America, Europe, India and Africa

| | Percentage of pigs infested | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | CANADA | | GREECE | INDIA | UNITED KINGDOM | | | | UNITED STATES OF AMERICA | | | | | AFRICA | | |
| | Quebec | Quebec | Northern Greece | Bihar | Wales | Scotland | Scotland | Scotland | South Eastern States | Wisconsin | Indiana | Indiana | South Carolina | Nigeria | South Africa Transvaal | South Africa Transvaal |
| | Martin et al. (1974) | | Himonas & Triantaphyllou (1972) | Sinha (1968a) | Jenkins & Erasmus (1963) | Jacobs & Dunn (1969) | | | Spindler (1934)* | Goldsby & Todd (1957) | Gaafar (1961) | Bennett & Copeman (1970) | Riddle & Forrester (1972) | Fabiyi (1979) | Farmers | Specula= tors |
| Mass | Market weight | Mature swine | - | - | - | 41 kg | 72 kg | Adults | > 90 kg | Market weight | < 110 kg | 16,1 kg | Brood sows & market hogs | Mixed | < 100 kg | < 90 kg |
| All helminths | - | - | - | - | 88,9 | - | - | - | 100,0 | 100,0 | 79,2 | 95,1 | - | 89,0 | 73,1 | 100,0 |
| *Ascaris* | 38,9 | 2,9 | 36,7 | 23,4 | 40,7 | 34,2 | 28,6 | 11,4 | 74,0 | 65,4 | 48,4 | 64,6 | 0 | 58,2 | 30,8 | 7,7 |
| *Ascarops* | 0 | 0 | 11,4 | 55,5 | 0 | 0 | 0 | 0 | 53,0 | 46,5 | 17,4 | 19,1 | 43,0 | 67,1 | 65,4 | 92,3 |
| *Globocephalus* | 0 | 0 | 14,6 | 0 | 0 | 0 | 0 | 1,4 | 11,0 | 0 | 0 | 1,6 | 0 | 11,1 | 0 | 0 |
| *Hyostrongylus* | 0 | 35,3 | 0 | 0 | 0 | 0 | 0 | 50,7 | 15,0 | 49,5 | 22,6 | 0 | 0 | 31,8 | 0 | 0 |
| *Macracanthorhynchus* | 0 | 0 | 3,2 | 0 | 0 | 0 | 0 | 0 | 25,0 | 5,9 | 3,7 | 6,1 | 7,0 | 0 | 0 | 0 |
| *Metastrongylus* | N E | N E | 43,1 | 2,0 | 40,7 | N E | 5,6 | 15,0 | 69,0 | 55,8 | N E | N E | 23,0 | 75,8 | 3,8 | 0 |
| *Oesophagostomum* | 25,6 | 67,6 | 32,4 | > 81,0 | 40,0 | 67,0 | 43,0 | 94,0 | 100,0 | 77,2 | 51,9** | 47,1 | 57,0 | > 83,6 | 26,9 | 11,5 |
| *Physocephalus* | 0 | 0 | 20,0 | 44,2 | 0 | 0 | 0 | 0 | 47,0 | 19,8 | 2,2 | 1,2 | 14,0 | 15,1 | 0 | 65,4 |
| *Strongyloides* | 0 | 0 | 9,7 | 0 | 0 | 0 | 0 | 0 | 26,0 | 13,9 | 0 | N E | N E | 13,3 | 0 | 0 |
| *Trichostrongylus* | 0 | 0 | 14,6 | 0 | 0 | 0 | 0 | 1,4 | 0 | 0 | 0 | N E | 0 | 0 | 15,4 | 7,7 |
| *Trichuris* | 13,3 | 0 | 6,5 | 4,6 | 63,6 | 42,0 | 29,4 | 14,3 | 23,0 | 13,9 | N E | 77,2 | 15,0 | 36,7 | 15,4 | 11,5 |

N E = Not examined

* Cited by Bennett & Copeman (1970)

** Based on lesions in the intestinal wall or parasites in the contents in the present survey.

The combined results of all pig stomachs examined in this survey and those of surveys conducted in India and the Philippines, in which stomachs only were examined, are summarized and compared in Table 6.

The incidence of infestation with *Ascarops strongylina* in farm pigs (58,3 %) was similar to that encountered in India (56,5 %) and the Philippines (45,1 %), while that of *Physocephalus sexalatus* (2,1 %), though similar to that in the Philippines (3,0 %), was considerably lower than that in India.

The incidence of the above parasites in pigs marketed by speculators exceeded that in both India and the Philippines.

*Simondsia paradoxa* was encountered in India, and *Hyostrongylus rubidus* and *Gnathostoma doloresi* in the Philippines, but were absent in this survey.

## Discussion

The pigs originating from farms could have been subjected to various forms of management and housing. They would most probably have been kept in concrete-floored pens, regularly or irregularly cleaned, or on earth in small or large pens, in large paddocks with or without vegetation, or on free range.

The pigs marketed by speculators, however, would probably have been reared in the most primitive conditions, either in earthern floored large pens, in paddocks or on free range.

Housing pigs in concrete-floored pens which are regularly cleaned should eliminate the possibility of helminth infestation. The stomach worms, *Ascarops strongylina* and *Physocephalus sexalatus*, are notable exceptions because dung-beetles, their intermediate hosts, could readily enter or leave the pens.

In small earth-floored pens the chances of *Ascaris suum* and *Trichuris suis* infestation are much greater as infestation is concentrated in a small area and pigs are inclined to root in the earth of these pens and

TABLE 6 Survey 1. The percentage of pigs with stomach helminths in India, the Philippines and South Africa

| Country | No. of stomachs examined | Incidence of infestation % | | | | |
|---|---|---|---|---|---|---|
| | | *Ascarops strongylina* | *Physocephalus sexalatus* | *Hyostrongylus rubidus* | *Simondsia paradoxa* | *Gnathostoma doloresi* |
| India (Sinha, 1968b) | 154 | 56,5 | 44,2 | 0 | 29,9 | 0 |
| Philippines (Tongson *et al.*, 1971) | 1 011 | 45,1 | 3,0 | 23,4 | 0 | 2,3 |
| S.A. Farmers | 48 | 58,3 | 2,1 | 0 | 0 | 0 |
| S.A. speculators | 46 | 91,3 | 58,7 | 0 | 0 | 0 |

S.A. = South African

thus readily ingest eggs containing infective larvae.

Large pens or paddocks favour all types of nematode infestation but, because of the more extensive form of confinement, *Ascaris suum* and *Trichuris suis* will play a lesser role, as pig faeces and hence infesta= tion may be concentrated in the pigs' dunging area and become dissemi= nated only as the dung breaks up and is spread. The larvae of *Trichostrongylus* spp. and *Oesophagostomum* spp. will have a better chance of reaching the infective stage under these conditions, whereas in smaller pens they would be either eaten, trampled, exposed to direct sunlight or buried before reaching this stage of development.

On free range pig excreta will naturally be deposited over large areas and the dung-beetles which serve as intermediate hosts of the larvae of *Ascarops strongylina* and *Physocephalus sexalatus* will afford these species greater chance of survival until they have reached the infective stage than would be the case in a more confined space. In addition, human and canine excreta are frequently present on free range, and in this way pigs may become infected with tapeworm cysts.

The stomach worm *Hyostrongylus rubidus* was recovered in many of the overseas surveys and in Nigeria. The results of those conducted in Scotland by Jacobs & Dunn (1969), the United States of America by Bennett & Copeman (1970) and in Nigeria by Fabiyi (1979) suggest that it is a parasite of older pigs. Few pigs of breeding mass were examined in the present survey and therefore the presence of this nematode cannot be excluded, although there is no previous record of its recovery in South Africa.

The recovery of *Trichostrongylus colubriformis* is a new record for pigs in South Africa. The fact that it was found in six of the pigs examined indicates that it is fairly common and that its presence must have been overlooked rather than that it has only recently acquired the pig as a host. It was recorded for the first time in pigs in Hungary by Kotlán & Von Mócsy (1933), in Britain by Dunn & Jacobs (1966) and in Greece by Himonas & Triantaphyllou (1972).

The recovery of *Oesophagostomum quadrispinulatum* is also a new record for South Africa. It is probable that in common with England (Taffs, 1967) this parasite occurs in many areas in the RSA.

The lungworm *Metastrongylus apri* is a new record for the Transvaal. It is interesting that the only pig found to be infested with this parasite in this survey came from a district of the Transvaal where the climate is generally considerably cooler and moister than that in the remainder of the Province which agrees with the findings of Rose (1959) that it generally prefers cool and moist conditions.

It was at first thought that the gastric ulcers observed were caused by infestations with *Ascarops strongylina* and *Physocephalus sexalatus*, but they were frequently encountered in pigs harbouring neither of these worms, while a pig with more than 5 800 stomach worms exhibited no visual gastric abnormalities. These stomach ulcers were probably instead due to one or more of the numerous causes listed by Kowalczyk (1969) in his review of the aetiology of gastric ulcers in swine.

The high incidence of stomach ulceration in pigs marketed by speculators could possibly be due to stress, as pigs from various sources are purchased, transported and even housed together for a short period prior to marketing, and may thus be subjected to conditions of overcrowding and severe stress. It has been shown that stress can precipitate the initiation of gastric ulcers in swine (Kowalczyk, 1969), as is the case in man.

*Survey 2. Semi-intensive housing. Boekenhoutkloof*

Materials and Methods

This survey was conducted on a pig and poultry farm in the Boekenhoutkloof area. The piglets were born, raised and prepared for market in concrete-floored pens that were regularly cleaned. The boars and also the sows, after their piglets had been weaned and until just before they farrowed again, were maintained in camps with earth floors. The only anthelmintic known to have been used on the farm was Hygromycin administered with feed for a few months during 1966 and 1967.

Before the start of the survey numerous faecal examinations done on piglets, weaners, sows and boars gave negative results. Five stunted piglets which had been reared in a pen with an earth floor were found at necropsy to harbour only *Trichuris suis*.

On 14 February 1968 six newly-weaned piglets and two pregnant sows were placed in an earth-floored pen, 200 $m^2$ in area. The sows and two of the piglets once they had become infested, were to remain in the pen and to serve as a source of infestation, but the two piglets died within two months and were not replaced. The other four piglets were to serve as tracers. When the sows were about to farrow they were replaced by two other sows.

The pigs were fed a proprietary feed, and water was supplied in a cement drinking trough that frequently overflowed and formed a muddy patch.

Two of the four tracer piglets introduced originally were slaughtered after being in the pen for one month and two newly-weaned piglets were introduced at the same time. Thereafter two newly-weaned piglets were introduced at monthly intervals and slaughtered after being two months in the pen, which allowed a period of one month overlap between successive pairs. The sows were removed during August 1968 after the level of infes= tation within the pen had built up to a satisfactory level. In November the pen size was reduced to 100 $m^2$.

From August 1968 onwards four piglets were introduced each month, two to be slaughtered after one month and the other two after two months. The last tracer piglets were slaughtered on 20 March 1969 and at the same time two previously unexposed piglets were slaughtered.

On the day prior to slaughter the piglets were transported to the laboratory and starved overnight. At necropsy the following morning, after the presence of milkspot lesions in the livers had been noted, the lungs, livers and gastro-intestinal tracts were processed for helminth recovery.

Until November 1968 mucosal scrapings of the entire gastro-intestinal tracts were digested with pepsin and hydrochloric acid. Thereafter mucosal scrapings of the small and large intestines only were digested, while stomach mucosae were thoroughly scraped and the scrapings processed with stomach ingesta in a waterbath. From November 1968 onwards 1/10 to 1/8 of each liver by mass was also subjected to pepsin/HCl digestion.

## Results

The total worm burdens of individual pigs and presence of liver lesions are presented in Table 7. For convenience the pigs are consecutively numbered in the order in which they were exposed.

Seven nematode species were recovered; of these *Trichuris suis* was the most abundant, followed by *Ascarops strongylina* and *Ascaris suum*.

*Ascarops strongylina*: Small numbers of worms were recovered from individual pigs slaughtered from March to October 1968. Larger numbers of parasites were recovered from most pigs slaughtered from November until the completion of the survey in March 1969.

*Trichostrongylus colubriformis*: Two adult worms only were recovered, from a single pig slaughtered during July 1968.

*Ascaris suum*: Infestation with this species was absent in the eight pigs slaughtered during March to June 1968. During July to October, six of 11 pigs slaughtered were infested with fourth stage larvae or adult worms. Of the remaining 17 tracer pigs slaughtered, 16 were infested, ten of these harbouring third stage larvae in their intestines. The greatest number of adult worms recovered from a single pig was 18 and the largest total burden consisted of 88 third and fourth stage larvae. Once *A. suum* infestation had become established in the pen, liver lesions were encountered in nearly all pigs.

*Oesophagostomum dentatum*: Three piglets were infested with adult worms of this species, but no immature worms were recovered.

*Trichuris suis*: The majority of piglets slaughtered from March to August 1968 harboured fifth stage or adult worms. The level and incidence of infestation was markedly reduced during September and October, but rose sharply thereafter to continue at a high level until completion of the survey. Many immature worms were recovered during this latter period.

*Capillaria* sp.: Worms of this species were recovered only from those portions of livers subjected to pepsin/HCl digestion. As only immature worms were recovered, specific identification was not possible.

TABLE 7 Survey 2. The worm burdens of tracer piglets slaughtered at Boekenhoutkloof in the Pretoria District between March 1968 and March 1969

| Pig No. | Date | | No. of helminths recovered | | | | | | | | | | Liver lesions |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Exposed | Slaughtered | *Ascarops strongylina* | | | *Ascaris suum* | | | *Oesophagostomum dentatum* | *Trichuris suis* | | *Capillaria* sp. | |
| | | | 3rd | 4th | Adult | 3rd | 4th | Adult | Adult | Immature | Adult | | |
| 1 | 14 Feb. 68 | 15 Mar. 68 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | - | o |
| 2 | 14 Feb. | 15 Mar. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | o |
| 3 | 14 Feb. | 17 Apr. | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 0 | 29 | - | o |
| 4 | 14 Feb. | 17 Apr. | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 34 | - | o |
| 5 | 14 Mar. | 17 May | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 75 | - | o |
| 6 | 14 Mar. | 17 May | 0 | 0 | 0 | 0 | 0 | 0 | 18 | 0 | 84 | - | o |
| 7 | 18 Apr. | 18 June | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 28 | - | o |
| 8 | 18 Apr. | 18 June | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 17 | - | o |
| 9 | 16 May | 17 July | 0 | 4 | 1 | 0 | 0 | 0 | 0 | 5 | 51 | - | o |
| 10* | 16 May | 17 July | 0 | 1 | 0 | 0 | 1 | 6 | 0 | 5 | 7 | - | o |
| 11 | 20 June | 14 Aug. | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 64 | - | +++ |
| 12 | 20 June | 14 Aug. | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 1 | 34 | - | ++ |
| 13 | 18 July | 10 Sep. | 0 | 2 | 0 | 0 | 3 | 6 | 0 | 7 | 19 | - | +++ |
| 14 | 15 Aug. | 10 Sep. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | o |
| 15 | 15 Aug. | 10 Sep. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | o |
| 16 | 15 Aug. | 15 Oct. | 0 | 0 | 1 | 0 | 2 | 3 | 0 | 3 | 2 | - | + |
| 17 | 15 Aug. | 15 Oct. | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 5 | 4 | - | + |
| 18 | 12 Sep. | 15 Oct. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | o |
| 19 | 12 Sep. | 15 Oct. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | - | o |
| 20 | 12 Sep. | 13 Nov. | 0 | 5 | 12 | 19 | 53 | 0 | 0 | 292 | 70 | 8 | ++++ |
| 21 | 12 Sep. | 13 Nov. | 0 | 0 | 0 | 1 | 4 | 0 | 0 | 158 | 115 | 8 | ++++ |
| 22 | 17 Oct. | 13 Nov. | 0 | 0 | 1 | 38 | 50 | 0 | 1 | 48 | 24 | 4 | ++++ |
| 23 | 17 Oct. | 13 Nov. | 0 | 46 | 77 | 27 | 53 | 3 | 0 | 18 | 83 | 4 | ++ |
| 24 | 17 Oct. | 11 Dec. | 3 | 7 | 91 | 2 | 1 | 0 | 0 | 33 | 380 | 0 | +++ |
| 25 | 17 Oct. | 11 Dec. | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 132 | 864 | 40 | +++ |
| 26 | 14 Nov. | 11 Dec. | 0 | 0 | 0 | 0 | 7 | 1 | 0 | 52 | 144 | 10 | +++ |
| 27 | 14 Nov. | 11 Dec. | 0 | 0 | 2 | 31 | 23 | 0 | 0 | 45 | 97 | 11 | ++++ |
| 28 | 14 Nov. | 14 Jan. 69 | 0 | 2 | 5 | 0 | 1 | 0 | 0 | 1 | 439 | 0 | + |
| 29 | 14 Nov. | 14 Jan. | 0 | 12 | 12 | 0 | 0 | 12 | 0 | 0 | 708 | 0 | ++ |
| 30 | 12 Dec. | 14 Jan. | 0 | 8 | 5 | 2 | 1 | 13 | 0 | 6 | 6 | 0 | + |
| 31 | 12 Dec. | 14 Jan. | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 18 | 39 | 0 | + |
| 32 | 12 Dec. | 20 Feb. | 1 | 16 | 67 | 0 | 1 | 18 | 0 | 170 | 322 | 40 | + |
| 33 | 12 Dec. | 20 Feb. | 12 | 49 | 34 | 0 | 1 | 0 | 0 | 99 | 169 | 10 | +++ |
| 34 | 16 Jan. 69 | 20 Feb. | 0 | 5 | 4 | 2 | 1 | 0 | 0 | 361 | 100 | 0 | +++ |
| 35 | 16 Jan. | 20 Mar. | 2 | 11 | 4 | 7 | 0 | 0 | 0 | 20 | 171 | 0 | ++ |
| 36 | 16 Jan. | 20 Mar. | 0 | 4 | 25 | 1 | 0 | 0 | 0 | 4 | 104 | 0 | +++ |
| 37 | Weaner | 20 Mar. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | o |
| 38 | Weaner | 20 Mar. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | o |

* Two adult *Trichostrongylus colubriformis* recovered

o = No liver lesions

\+ = Few liver lesions

++++ = Very many liver lesions

General: The two newly-weaned piglets that had been raised in a manner similar to the tracer piglets before exposure were free from helminth infestation.

Temperature and rainfall data obtained from two weather stations within a 5 km radius of Boekenhoutkloof are graphically reproduced in Fig. 3.

The highest maximum temperatures were recorded during January and February 1968 and 1969 and lowest minima during June and July 1968. Rainfall was virtually absent during June to September 1968.

## Discussion

The absence of infestation in the two newly-weaned piglets that had been subjected to the same form of management as tracer piglets before exposure indicates that the latter were indeed worm-free at exposure and that infestation was acquired during their sojourn in the earth-floored pen and not before. This finding also implies that farrowing and raising piglets in a regularly cleaned, concrete-floored pen is an excellent method of worm control.

### *Ascarops strongylina*

The virtual absence of this parasite in piglets slaughtered during winter and early spring is probably due to dormancy during these seasons of coprophagous beetles, its intermediate hosts. Development of larval stages within intermediate hosts during cooler months is probably also prolonged and thus the possibility of infestation is further reduced. During the summer months beetles are more abundant and development of helminth larvae to the infective stage would probably be accelerated and result in both a greater incidence of infestation and higher worm burdens.

### *Trichostrongylus colubriformis* and *Oesophagostomum dentatum*

Under the conditions prevailing in the experimental pen, free-living stages of these parasites could be either ingested, exposed to direct sunlight or buried under soil by rooting pigs before reaching the infective stage. This would account for the virtual absence of these genera in this experiment.

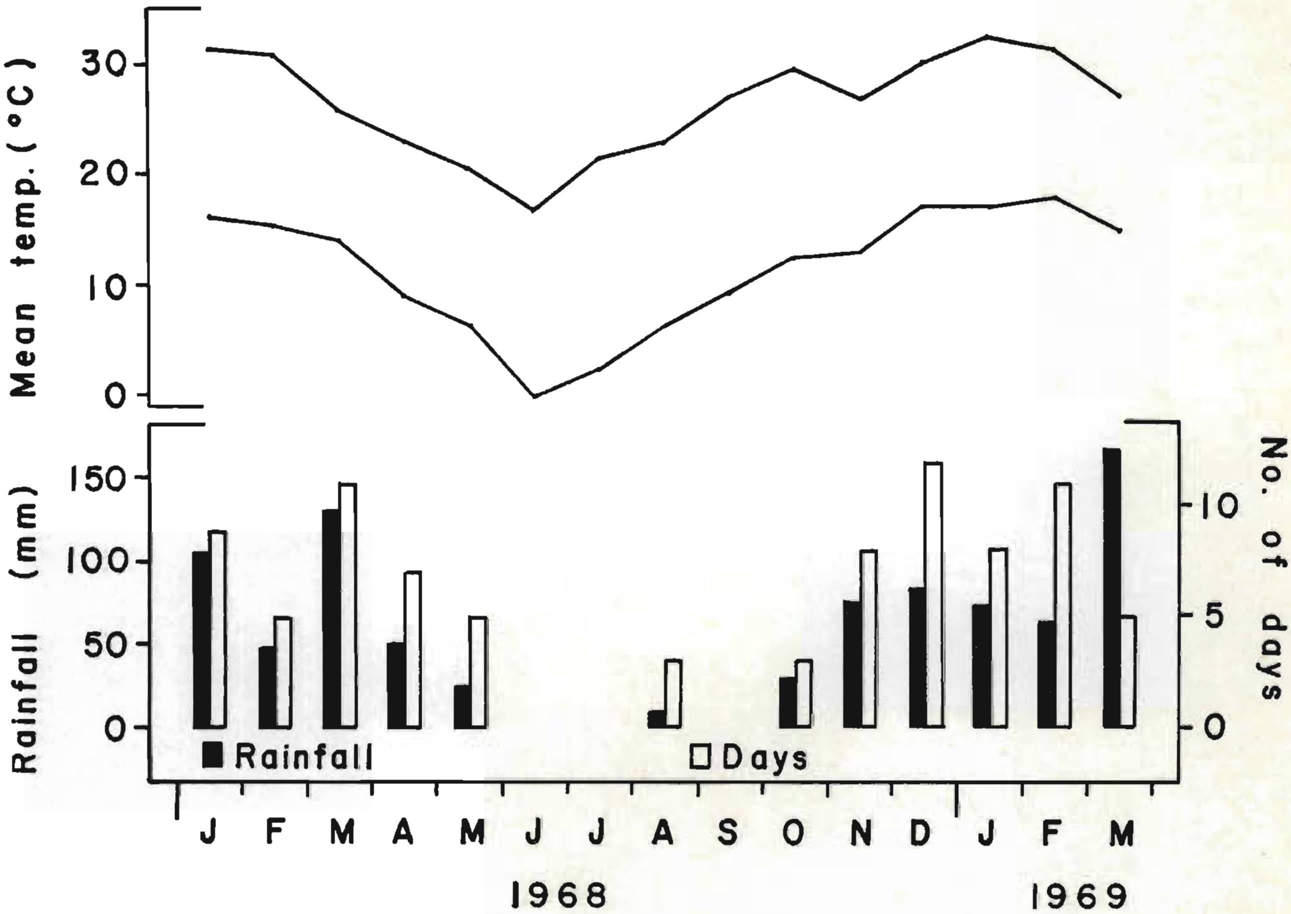



Fig. 3 Survey 2. Mean atmospheric temperature, rainfall and the number of days on which rain fell at two weather stations within a 5 km radius of the pig farm at Boekenhoutkloof in the Pretoria District

*Ascaris suum*

The first adult *A. suum* were recovered from a piglet slaughtered during July 1968 and these worms and those in the sows were therefore responsible for contaminating the pen and ensuring infestation of piglets subsequently introduced. The sudden increase in worm burdens during November 1968 is probably a reflection of increased temperature at that time resulting in the more rapid development of eggs to the infective stage.

Because eggs of this species are resistant to adverse conditions (Mönnig, 1934), it is almost impossible to eliminate this infestation once it has become established in an earth-floored pen. The worm burdens or liver lesions observed in nearly all piglets exposed after July 1968 show that the rooting habits of pigs ensure that virtually every animal will become infested.

Although *A. suum* infestation is frequently encountered in pigs (Jenkins & Erasmus, 1963; Sinha, 1968a; Bennett & Copeman, 1970; Himonas & Triantaphyllou, 1972; Fabiyi, 1979; Survey 1), its establishment in the intestine of this host after artificial infestation is extremely variable (Kelley, Olsen & Hoerlein, 1958; Schwartz, 1959; Green & Oldham, 1964). This variability is probably due to elimination of larvae from the small intestine at the time of the third moult, ten to 15 days after initial infestation (Douvres *et al.*, 1969) and to further elimination commencing 21 days after infestation (Schwartz, 1959). This may also be true in natural infestations particularly those acquired over a period, in which immunity may also play a role in eliminating infestation (Taffs, 1964).

The presence and severity of liver lesions in the present survey suggest that larger intestinal worm burdens should have been recovered and that elimination of larvae from the small intestinal tract was probably responsible for the small numbers of worms encountered. The recovery of third stage larvae from the small intestine is in agreement with the life cycle as described by Douvres *et al.* (1969).

*Trichuris suis*

The rate of development of larvae to the infective stage within the egg is dependent upon temperature. At temperatures between 31° and 34°C this stage is reached in 50 % of eggs in 19 to 20 days, while at 20°C development takes 102 days (Beer, 1973). The delay in development due to cold is reflected in the low incidence of infesta= tion in pigs slaughtered during September and October 1968. Although September and October are not the coldest months, larvae in the eggs deposited in the coldest months of the winter prior to this would not have developed to infectivity and this would account for the low incidence of infestation. The rapid increase in infestation from November onwards is probably due to large numbers of larvae simultaneous= ly developing to infectivity in eggs excreted during earlier cooler months and subsequently exposed to an increase in temperature.

No attempt was made to determine the numbers of larvae in the various stages of larval development, as development from first to fifth stage occurs within the host (Beer, 1973), and differentiation would be difficult. In contrast to Beer (1973) who found that larvae were recovered only from the caecum and colon, many larvae were recovered from the mucosa and ingesta of the small intestine.

*Capillaria* sp.

The worms recovered from liver digests may have been acquired from poultry, as dead birds were occasionally fed to the pigs, or from rats which were present in the pens. *Capillaria* spp. have not previously been recovered from pigs and the fact that only immature worms were recovered indicates that these parasites were probably in an abnormal host.

*General*

The conditions in the experimental pen suited the free-living stages of certain helminths. Both *Ascaris suum* and *Trichuris suis* develop to infectivity within the egg and these eggs can survive for exceptionally long periods. Thus, once these eggs are present burying, exposure or desiccation would not seriously affect their ability to infest pigs and it is logical that these parasites should predominate under these conditions.

Those helminths with free-living larval stages would be at a consider= able disadvantage because the exposed nature of the pen, complete absence of vegetation and rooting habits of the pigs would subject these larvae to extremely adverse conditions of dessication and solar radiation. The low incidence of *Oesophagostomum dentatum* and *Trichostrongylus colubriformis* can be ascribed largely to these factors.

Helminths such as *Ascarops strongylina*, which utilize a coprophagous beetle as intermediate host for the larval stages, would thus not be exposed to the adverse conditions in the pen. The pigs would then become infested by ingestion of these beetles, which would be attracted to the accumulation of faeces in the pen.

## CONTROL MEASURES

Effective control of nematode infestations can be obtained by keeping all pigs in concrete- or slatted-floor pens which are regularly cleaned. This was confirmed by the worm-free nature of the piglets housed in concrete-floored pens prior to use as tracers in the pen at Boekenhout= kloof. If pigs are kept in earth-floored pens anthelmintics should be used that can be administered with the feed or by injection, and are effective against *Ascaris suum*, *Trichuris suis* and *Oesophagostomum* spp. These anthelmintics are preferred because of ease of administration compared with compounds that have to be dosed orally to individual pigs. Treatments administered during October to May should control most species, but when *Ascaris suum* is present treatment throughout the year, particu= larly of piglets, may be necessary because of persistence of infestation in the soil of the pens.

Sows coming from earth-floored pens or from pasture into farrowing pens should be treated in concrete-floored holding pens to eliminate infestation 48 h prior to entering the farrowing pens. They should then be thoroughly washed down, particularly their udders and teats, to remove any adherent worm eggs immediately before being placed in the farrowing pens.

# *PART II HELMINTHS OF RUMINANTS*

## *HELMINTHS OF SHEEP*

### Introduction

The majority of wooled sheep in the RSA are concentrated in the western, south-western and eastern Cape Province, the Karoo and the eastern Highveld of the Orange Free State and Transvaal. The seasonal fluctuations of helminth burdens in sheep have been determined in the south-western Cape (Muller, 1968; Snijders, Stapelberg & Muller, 1971), Border and eastern Cape (Barrow, 1964; Rossiter, 1964) and Karoo (Viljoen, 1964, 1969).

On the Transvaal Highveld seasonal fluctuations in faecal worm egg counts have been reported by Thomas (1968), but no surveys based on actual worm burdens at necropsy have been conducted in this province. Nor have surveys in sheep grazed on irrigated pasture been carried out anywhere in the RSA.

The three surveys reported here were conducted in Merino sheep grazed on the Transvaal Highveld. Two were in sheep on irrigated pasture and one in sheep on dry-land pastures.

### *Surveys 3 and 4. Irrigated pasture. Hennops River*

### Materials and Methods

*Survey 3*

*Pastures*

The grazing at Hennops River consisted of grass/clover leys established during 1967 and 1968 and was divided into summer and winter pastures.

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

*Infestation and management*

Helminth infestation was introduced on to the newly established summer pasture by a naturally infested flock of 30 Dorper sheep purchased from a neighbouring farm and 115 Merino ewes purchased in the western Cape Province. The pasture was grazed from April 1968 to 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 tracer 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 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 ten 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 two 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 pasture. The sheep remained on the winter pasture until the end of September 1969.

From May to October 1969 two of the five fields of summer pasture previously grazed by the sheep were grazed by calves in Survey 6. Amongst other nematodes these calves were infested with *Cooperia pectinata* and *Cooperia punctata*.

The sheep were moved from the winter pasture during October 1969 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 three of the five fields utilized during the previous summer, but did not graze again those fields on which calves had been penned.

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

The pastures were irrigated by means of sprinklers on two to four 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 four to eight months old when placed on the pasture. They were introduced on to the pasture in pairs at approximately 28-day intervals from October 1968 to June 1970 and removed approximately 33 days later, thus allowing an overlap of five days between successive pairs.

*Flock lambs*

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

*Survey 4*

*Pastures*

During the entire survey period only four of the ten fields of summer grazing mentioned in Survey 3 were utilized.

*Infestation and management*

Five sheep belonging to the flock lambs in Survey 3 continued to graze these fields. These and other untreated sheep added to their number are henceforth referred to as flock sheep, and served to maintain infestation on the pastures.

From January until July 1971 40 lambs, 32 of which were treated with anthelmintics at various intervals, were placed on the pastures. From July 1971 onwards the number of flock sheep was gradually increased by the introduction of 30 untreated sheep, six of which were artificially infested with *Chabertia ovina*. Some of these sheep died while others were removed, leaving a total of eight flock sheep at the conclusion of the survey. During September 1972 approximately 70 Merino lambs, all of which were treated at various intervals with anthelmintics, were penned with the flock sheep until the conclusion of the survey.

From February 1971 to September 1972 worm egg counts were done at weekly intervals on the faeces of eight or more flock sheep. Thereafter the interval was increased to two weeks. On each occasion the faeces of the sheep were combined and a single faecal larval culture was made. From these cultures the mean monthly 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 to 07h00 the following morning.

Irrigation and fertilizer were applied as in the previous survey.

*Tracer lambs*

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

## Results

*Survey 3*

*Tracer lambs*

The mean worm burdens of the tracer lambs are summarized in Table 8.

Eleven helminth species were recovered. Of these *Haemonchus contortus* were the most abundant followed by *Ostertagia* spp. and *Trichostrongylus colubriformis*.

TABLE 8 Survey 3. The mean worm burdens of two tracer lambs slaughtered at each occasion from November 1968 to July 1970 on irrigated pasture at Hennops River on the Transvaal Highveld

| Date slaughtered | Mean numbers of helminths recovered at necropsy | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Haemonchus contortus* | | *Ostertagia* spp. | | *Trichostrongylus colubriformis* | | *Nematodirus spathiger* | | *Cooperia* spp. | *Oesophagostomum columbianum* | *Trichuris* spp. | *Dictyocaulus filaria* | *Moniezia 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

*Haemonchus contortus*: Peak burdens in excess of 1000 fourth stage larvae were recovered from the lambs slaughtered from March to May 1969 and from February to June 1970. Judging by their size the majority of these larvae were in the early fourth stage of development. Adult burdens reached a peak exceeding 200 worms from November 1969 to April 1970.

*Ostertagia* spp.: Both *O. circumcincta* and *O. trifurcata* were present, peak total burdens of approximately 300 or more worms being recorded generally during May or June and September to November.

*Trichostrongylus colubriformis*: Mean burdens exceeded 500 worms from April to June 1970.

*Nematodirus spathiger*: Peak burdens in excess of 70 worms were recovered during May to July 1970.

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

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

*Dictyocaulus filaria*: When worms of this species were present small numbers only were usually recovered, but from May to July 1970 worm burdens increased considerably.

*Moniezia expansa*: Mean burdens exceeding 15 cestodes were encountered in the lambs slaughtered from November 1969 to May 1970.

### *Flock lambs*

The mean monthly differential faecal worm egg counts of the untreated lambs, atmospheric temperature and monthly precipitation on the pastures are graphically represented in Fig. 4.

With the exception of December 1969 when *Ostertagia* spp. predominated, the rise and decline in the mean total egg count were due to fluctuations in the egg output of *Haemonchus contortus*. These counts reached a peak during March 1969 declined in April, rose again in May and fell markedly

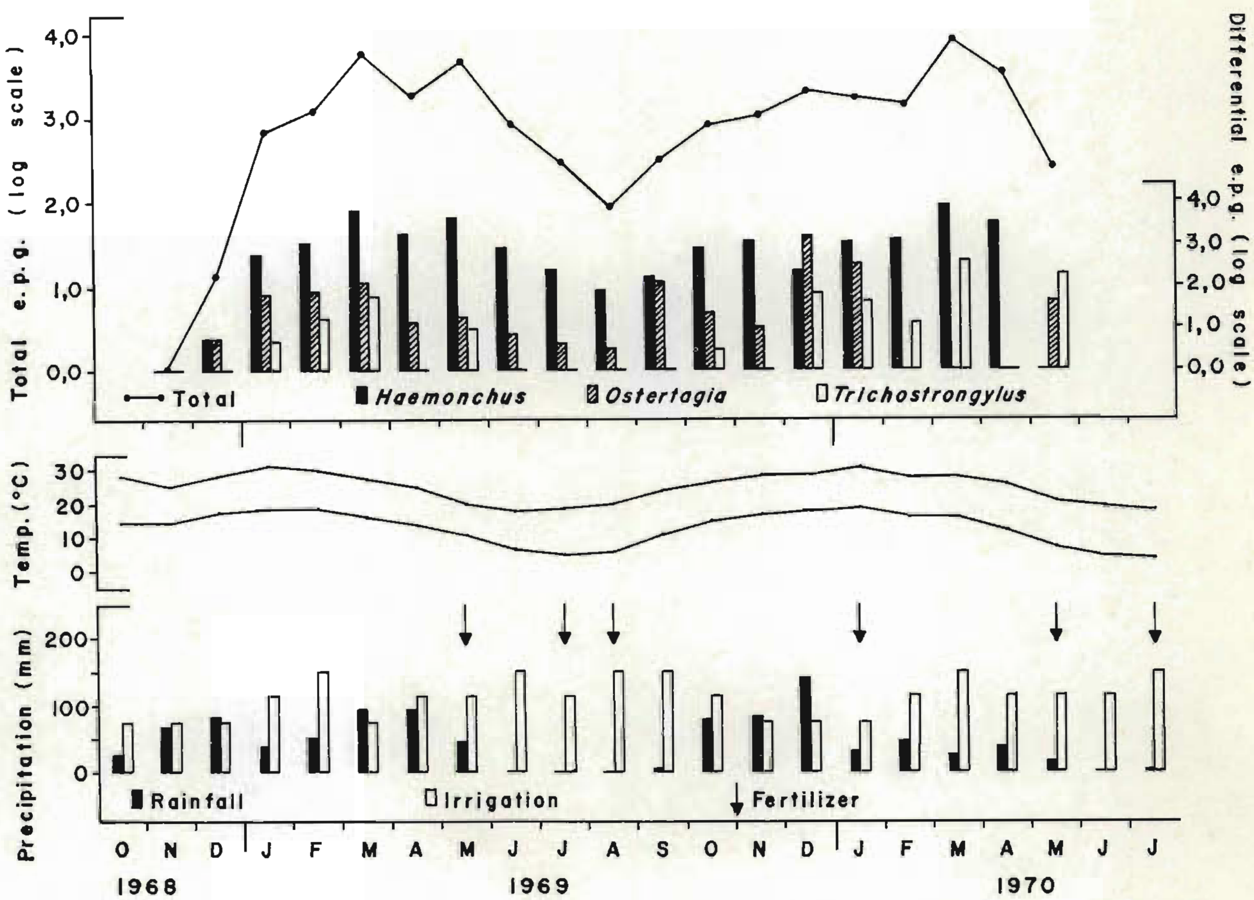



Fig. 4 Survey 3. Total and differential faecal worm egg counts (e.p.g.) of untreated flock lambs, atmospheric temperature, rainfall, irrigation and fertilizer applications on pastures at Hennops River on the Transvaal Highveld between October 1968 and July 1970

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.

Larvae of *Strongyloides papillosus* were recovered from faecal cultures during January and May 1969, those of *Cooperia* spp. during December 1969 and January 1970 and those of *Oesophagostomum columbianum* during January 1969 and May 1970. Eggs of *Nematodirus spathiger* were present in the faeces during March 1969 and first stage larvae of *Dictyocaulus filaria* were recovered from faeces during January, February and July 1969.

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

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

*Survey 4*

The mean worm burdens of the tracer lambs are summarized in Table 9, while the monthly mean differential faecal worm egg counts of the flock sheep, atmospheric temperature, rainfall and irrigation on the pastures are graphically illustrated in Fig. 5.

The mean monthly burdens of *Haemonchus contortus*, *Ostertagia* spp. *Trichostrongylus* spp. and *Moniezia expansa* recovered from lambs slaughter= ed in Surveys 3 and 4 and the percentage of fourth stage larvae of worms of the first two species are summarized in Table 10.

Eleven helminth species were recovered. *Haemonchus contortus*, *Ostertagia circumcincta* and *Trichostrongylus* spp. were the most abundant, while

TABLE 9 Survey 4. The mean worm burdens of three tracer lambs slaughtered at each occasion from April 1971 to May 1973 on irrigated pasture at Hennops River on the Transvaal Highveld

| Date slaughtered | *Haemonchus contortus* | | *Ostertagia circumcincta* | | *Trichostrongylus* spp. | | *Nematodirus spathiger* | | *Strongyloides papillosus* | *Oesophagostomum columbianum* | | *Chabertia ovina* | *Trichuris* spp. | *Moniezia 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 |

* Two lambs only slaughtered

4th = Fourth stage larvae

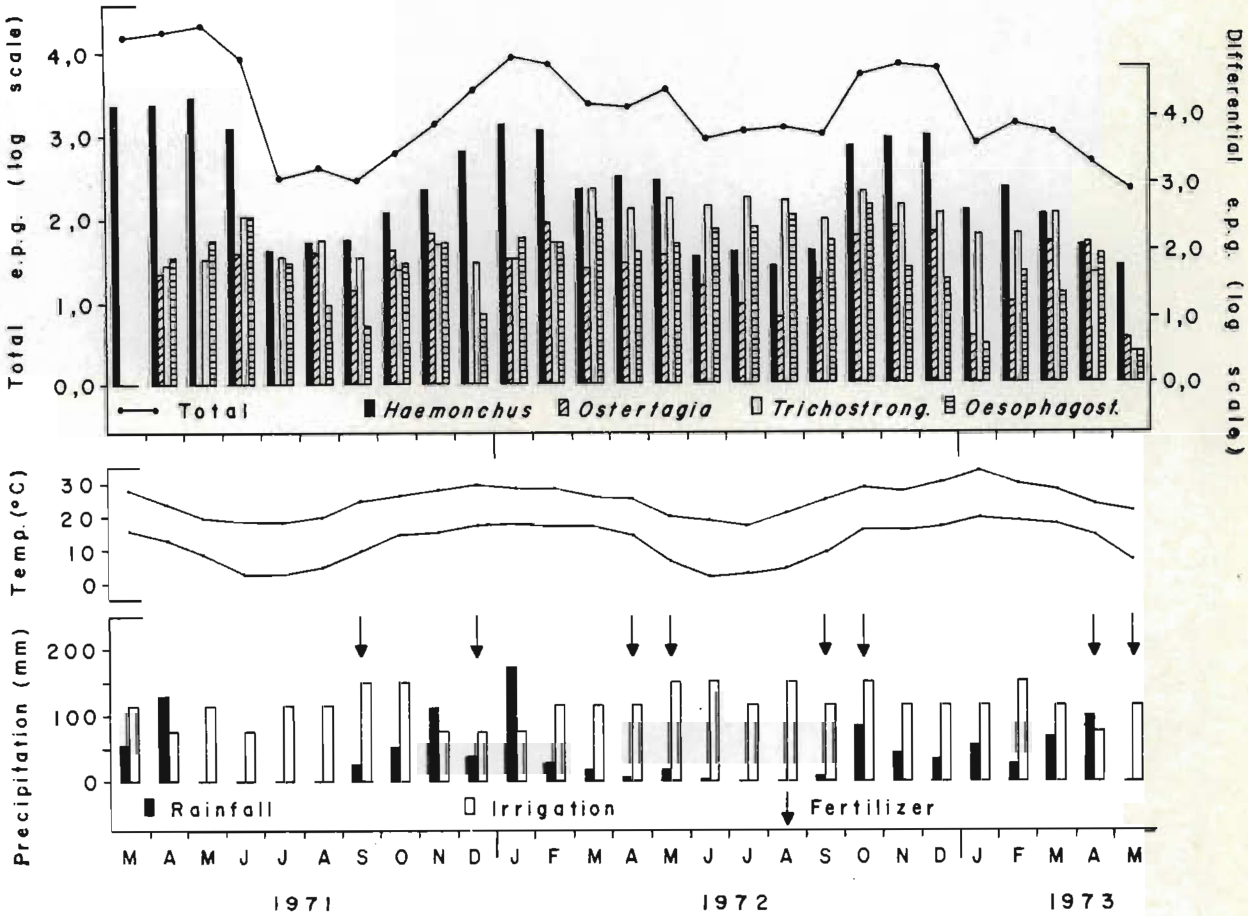



Fig. 5 Survey 4. Total and differential faecal worm egg counts (e.p.g.) of flock sheep, atmospheric temperature, rainfall, irrigation and fertilizer application on pastures at Hennops River on the Transvaal Highveld from March 1971 to May 1973

TABLE 10 Surveys 3 and 4. The mean monthly total burdens of the dominant helminth species and the percentage of fourth stage larvae of *Haemonchus contortus* and *Ostertagia* spp. Data derived from all tracer lambs slaughtered on irrigated pasture at Hennops River on the Transvaal Highveld between November 1968 and May 1973

| Month | Total No. of sheep slaughtered | Mean worm burdens | | | | | |
|---|---|---|---|---|---|---|---|
| | | *Haemonchus contortus* | | *Ostertagia* spp. | | *Trichostrongylus* spp. | *Moniezia 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 |

many *Nematodirus spathiger* and *Moniezia expansa* were also present.

*Haemonchus contortus*: Early fourth stage larvae predominated in lambs slaughtered during April and May in each year. Burdens in excess of 500 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 flock sheep during March to May 1971 and January, February, November and December 1972 (Fig. 5).

The mean percentage of worms in the fourth larval stage of development increased from 43,8 % during January until it reached 95,6 % during June. Thereafter it decreased to 10,1 % in November with a rise to 36,6 % in December (Table 10).

*Ostertagia circumcincta*: The largest total worm burdens were generally encountered in lambs slaughtered from April to October. During 1973 worm burdens remained at a particularly low level until the conclusion of the survey.

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

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

No *O. trifurcata* were recovered in Survey 4.

*Trichostrongylus* spp.: *T. colubriformis*, *T. falculatus* and *T. rugatus* were recovered, but the exact number of each species was not determined. The greatest numbers of worms were generally encountered from April to August in each year of the survey.

Faecal worm egg counts of the flock sheep reached a peak during June 1971, March to December 1972 and 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 burdens in excess of 40 worms were recovered from the lambs slaughtered during April and May 1972 and May 1973.

The flock sheep had peak faecal worm egg counts during May and June 1971 and January to March and June to October 1972.

*Moniezia expansa*: Worm burdens varied considerably between individual lambs but the largest numbers were generally recovered from lambs slaughtered between November and May. The greatest number of scolices recovered from a single lamb was 788.

Mean maximum temperatures exceeded 25°C from October or November to February or March and mean minimum temperatures fell below 5°C from June to August. Rainfall was generally low or absent from May to 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 water to the pastures by regular sprinkler irrigation large= ly eliminated 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 10 presents a summary of these findings for the four major genera.

The sheep were starved for 48h prior to slaughter, and the helminths recovered at necropsy were thus two to 35 days old. This must be taken into consideration when an estimate is made of the percentage of fourth stage larvae which should theoretically be present.

*Haemonchus contortus*

The third moult in this species occurs 1½ days and the fourth moult from nine to 11 days after infestation (Veglia, 1915). If the same level of infestation was acquired every day from the pastures, there should theoretically be very few third stage larvae in the tracer lambs at slaughter and fourth stage larvae should only account for 7/33 (21,2 %) of the worm burden. With the exception of November when fourth stage larvae comprised only 10,1 % of the total infestation, the percentage of worms in this stage of development always exceeded 36 % (Table 10).

From April to July fourth stage larvae accounted for more than 90 % of the worms recovered. This retardation in the fourth 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 was as high during July, when the total burden was considerably lower. These findings are in general agreement with those of Southcott, Major & Barger (1976) in New South Wales, Australia, except that they recovered peak numbers of *H. contortus* from tracer lambs grazed from January to March, that is prior to the onset of maximum larval retardation.

The phenomenon of arrested development accounts for this extension of the life cycle in the fourth 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 *Ostertagia* spp. infestations in sheep by James & Johnstone (1967), Connan (1971) and Reid & Armour (1972), and in *Haemonchus contortus* by Muller (1968), Connan (1971), Blitz & Gibbs (1972b), Brunsdon (1973) and Waller & Thomas (1975). It has been suggested by Armour & Bruce (1974) that this phenomenon corresponds to diapause in insects.

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

A further factor in the prolongation of the length of a complete life cycle is the apparent time-lag between maximum contamination of the pastures with eggs and subsequent availability of larvae. During 1971 maximum faecal worm egg counts were recorded in eight untreated lambs from March to May and maximum *H. contortus* burdens in tracer lambs during April and May. Maximum worm egg counts in the flock 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 encountered only 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. In north-east England Waller & Thomas (1975) found a delay of approximately two months between spring pasture contamination and larval availability, 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 burdens 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 first and second stage larvae survived because of the cooler conditions and thus more third stage larvae became available until the temperature dropped too low for further larval development.

The prolonged period of arrested larval development could mean that certain worms would complete only one life cycle a year, an observation made by Connan (1971) in the south of England and Waller & Thomas (1975) in north-east England. Other worms, less prone to inhibition, could complete two or more life cycles in a year. This variation in development within a population has been discussed by Michel (1974), and corresponds to the occurrence of univoltine, bivoltine and multivoltine strains of insects within a single population.

In the flock lambs and flock sheep a marked drop in the egg output 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 of both 1969 and 1971 was probably due to the maturation of overwintering fourth stage larvae, subsequently 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 the tracer lambs harbouring a mean of only 13 to 22 *H. contortus* (Table 9). The ingestion of the first substantial numbers of infective larvae during January 1973, however, coincided with a fall in faecal worm egg counts that persisted for the remainder of Survey 4.

As none of the flock sheep were slaughtered it was not possible to determine whether or not the decreases in faecal egg counts were due to an elimination of adult *H. contortus*.

*Ostertagia* spp.

*Ostertagia circumcincta* undergoes the third moult three days after infestation and the fourth moult five to six days later (Denham, 1969). Thus at slaughter, after 48h of starvation, the tracer lambs should still have harboured a few third stage larvae. It is possible that these were present but not recovered because of their low numbers and small size and the use of techniques which were perhaps not sensitive enough to ensure their recovery.

Provided equal numbers of larvae had been acquired on a daily basis fourth larval stages should have accounted for 6/33 (18,2 %) of the total popula= tion at slaughter. A ratio of immature to adult worms approximating the above percentage was recorded in sheep slaughtered from October to December (Table 10). At all other times the greater percentage of worms present as fourth stage larvae indicated arrested development. The proportion of arrested larvae was not dependent upon the number of worms present. In August and October the mean total worm burdens were practi= cally identical, despite this the highest percentage of arrested development was recorded in August and the lowest in October. The worm burdens in both these months were very modest and it is unlikely that population pressure would in any event have played a role in retardation of larval development.

Arrested development in *Ostertagia* spp. infestations occurred later and ceased sooner than the same phenomenon in *Haemonchus contortus*. The proportion of arrested larvae was hardly ever as large as in *H. contortus* and maximum retardation of 72,5 % of worms was encountered only 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), *Ostertagia* spp. in the warmer regions of the southern hemisphere favour the cooler months of the year, from autumn until spring, for development on the pastures. Because of this natural preference for cooler conditions, pressure to overwinter as arrested fourth stage larvae will be lower and will occur later than for *Haemonchus contortus*, which in these surveys preferred the warmer months from December to May for development on the pastures. Where the climate is colder, however, as in Cambridge, England the largest worm burdens are encountered during summer and autumn and the greater necessity to overwinter in the host animal results in the virtual cessation of development at the fourth larval stage during the winter months (Connan, 1971).

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

Because of its preference for cooler conditions the particularly warm weather experienced during December 1972 and January 1973 probably played a considerable role in reducing the availability of infective larvae of *Ostertagia circumcincta* to tracer lambs during 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 infective larvae of all species they were contributing little to further pasture contamination as they were treated with anthelmintics at intervals of four weeks. This probably had a particularly adverse effect on *O. circumcincta* as egg counts of this species in the flock lambs were very low during January and February 1972 and pasture recontamination was consequently already at a low level.

*Trichostrongylus* spp.

In Survey 3 only *T. colubriformis* was recovered, while in Survey 4 this species as well as *T. falculatus* and *T. rugatus* were encountered.

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

The peak *Trichostrongylus* spp. worm burdens encountered during April and May of both 1972 and 1973 were preceded in each year by a rise in the egg counts of *Trichostrongylus* spp. in the flock sheep. Despite the fact that these egg counts remained at a fairly high level until November 1972 infestation acquired from the pasture decreased from June onwards, when the temperature at soil level was probably unfavourable for development of the majority of eggs and larvae. Levine & Andersen (1973) have shown that larval development is essentially nil below a mean weekly maximum temperature of 10,0°C at soil level and poor between 10,0°C and 14,9°C. The atmospheric temperatures illustrated in Fig. 5 can serve as only 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 70 to 100 mm of grass.

The increased worm burdens during April and May confirm the observations of Muller (1968) that the free-living stages of this genus thrive during cool, moist conditions.

*Cooperia* spp.

The *Cooperia* spp. infestations in Survey 3 were acquired from the pasture on which calves in Survey 6 had grazed. Those present in lambs slaughter=ed in September and October 1969 had probably been acquired when the lambs passed through the pasture grazed by the calves, on the way to their own pasture.

*Oesophagostomum columbianum*

The numbers of worms recovered were generally very modest and the conclusions drawn are based only on peak burdens. The composition of the pastures may be the cause of the modest worm burdens as Southcott (1955) has demonstrated that *O. columbianum* are evacuated from sheep grazing green oats or clover pastures.

The recovery of *O. columbianum* in Survey 4 after its virtual disappearance in tracer lambs slaughtered during the latter half of Survey 3 indicates that this parasite may take a particularly long time to become established on artificial pastures. The long prepatent period of this parasite (Veglia, 1928), and the comparatively small numbers of adults generally recovered (Barrow, 1964; Rossiter, 1964), would contribute considerably to this phenomenon. This long prepatent period and regular use of highly effective anthelmintics at intervals shorter than the prepatent period probably account for the virtual absence of *O. columbianum* in many regions of the RSA where it had previously occurred.

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 more larvae per unit mass of feed were thus available. This seems to apply to other genera too but, whereas the considerable drop in temperature during May would retard or prevent the development of *O. columbianum* and *Haemonchus contortus* to the infective stage on the pastures, nematodes such as *Ostertagia circumcincta* and *Trichostrongylus* spp., which prefer cooler conditions, were still recovered in subsequent months.

*Dictyocaulus filaria*

The increase of *D. filaria* infestation in lambs slaughtered in Survey 3 during May to July 1970 may be due to two factors. Firstly, the cooler conditions were favourable for the free-living stages (Rose, 1955), and secondly the introduction of 18 worm-free Merino and 14 worm-free Karakul lambs during March and May resulted in increased pasture contamination once these lambs had become infested. 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, after they became infested, boost pasture contamination and result in increased burdens in the tracer lambs. During July 1970 two Karakul lambs succumbed to massive *D. filaria* infestations, which indicated that infestation continued to increase during the winter months.

No attempt was made to recover larval stages of *D. filaria* from lymph glands of the tracer lambs using the techniques 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 lambs slaughtered in Survey 4, the result probably of the removal of all susceptible sheep from the pasture during the months between the two surveys. The remaining flock lambs had probably acquired a solid immunity because of prolonged exposure to infestation and were thus incapable of recontaminating the pastures.

*Moniezia expansa*

The seasonal incidence of this cestode is largely dependent on the number of infested oribatid mites which act as intermediate hosts. The fact that 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 10). 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 pasture is due to their ingestion of overwintering oribatid mites containing tapeworm cysticercoids.

During December and January day length and atmospheric temperature both increase and the mites, which prefer dark, cool conditions, are probably available on the pasture only from late afternoon until early morning (Soulsby, 1965). As sheep in these surveys were usually 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 again increased.

*General*

With slight species variations, lower levels of infestation of most nematode species were encountered in tracer lambs slaughtered from September to December. In Victoria, Australia, Anderson (1972) considered it significant that larvae tended to disappear rapidly from the pasture when mean temperatures exceeded 15,5°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 the disappearance of larvae. At Hennops River solar radiation must be considered as a stress factor from September to November as pasture regrowth begins only in September, rainfall may be sparse and cloud cover is poor.

### *Survey* 5. *Dry-land pasture. Tonteldoos*

#### Materials and Methods

*Locality*

This survey, conducted on the farm "Houtenbek" near Tonteldoos, was carried out as part of a production trial in sheep, which has been reported elsewhere (Horak, Honer & Schröder, 1976).

*Flock lambs*

During the survey, helminth infestation was maintained on the pastures by a group of approximately 90 lambs of both sexes which were treated once only on 18 May 1973 at the start of the production trial, when they were approximately ten weeks old with rafoxanide and thiabendazole to rid them of *Oestrus ovis* and helminth infestations. These lambs, designated flock lambs, served as untreated control lambs for the duration of the production trial and grazed with a flock varying in number between 400 and 950 lambs. Ninety of the latter lambs were treated with cambendazole or thiabendazole and rafoxanide at 28-day intervals and served as a comparatively parasite-free group in the production trial. The remainder were treated with cambendazole during August and October 1973, thiabendazole during December 1973, May, August and October 1974, and rafoxanide during November 1973, February, April, June and November 1974, a treatment regime calculated to keep helminth and *O. ovis* infestation at a low level for the duration of the production trial.

*Husbandry and pastures*

All lambs were weaned on 26 July 1973 and thereafter subjected to the normal rotational grazing regime practiced on the farm. They were transferred to a small camp planted to Kikuyu grass (*Pennisetum clandestinum*) where their diet was supplemented with lucerne hay and maize meal. On 19 September they were put out on an *Eragrostis curvula* pasture from which, after being inoculated against enterotoxaemia, they were moved on 17 October 1973 to a pasture consisting of natural veld grasses. On 29 May 1974 they were shifted to a rested *E. curvula* pasture whence they were returned to the Kikuyu camp on 19 July. They were again put out on natural pasture on 3 October 1974 where they remained until the conclusion of the survey.

Faecal samples from the same ten ewe- and ten ram-lambs from amongst the flock lambs were collected and examined for nematode eggs at 14-day intervals and faecal cultures were made for larval differentiation.

*Tracer lambs*

At intervals of four weeks groups of three, four- to ten-month-old lambs born and raised under worm-free conditions were treated with thiabendazole and rafoxanide and housed indoors for the next four weeks to prevent infestation. From July 1973 to November 1974 these groups of three lambs were placed with the lamb flock at Tonteldoos at approximately 28-day intervals and removed after 42 days, thus allowing an overlap of 14 days between successive groups.

*Climate*

Daily minimum and maximum atmospheric temperature and rainfall were not recorded. Rain generally falls from September to May and a mean of 850 mm is registered annually. Because of the higher altitude, atmospheric temperatures are considerably lower than those recorded at Hennops River.

## Results

A number of tracer lambs died as they failed to adapt to conditions on the pastures and consequently, on certain occasions, only one or two lambs were available for necropsy.

The mean worm burdens of each set of tracer lambs are summarized in Table 11.

The mean monthly total burdens of *Haemonchus contortus* and *Ostertagia circumcincta* and the percentage of these worms in the fourth stage of larval development from November 1973 onwards are summarized in Table 12.

The mean monthly faecal worm egg counts and differential egg counts of the untreated control flock lambs are presented in Fig. 6.

Although 15 helminth species were recovered from the tracer lambs only those most commonly encountered are included in Table 11.

Very few parasites were recovered from either the two flock lambs slaughtered in May before the start of the survey or the first three groups of tracer lambs. *Trichuris* spp., however, were recovered in fair numbers from lambs slaughtered during September and October.

*Haemonchus contortus*: Total worm burdens increased in the lambs slaughtered from December 1973 onwards and, having reached a peak of 4 681 worms during April 1974, declined rapidly thereafter. They rose again during January 1975 when the survey ended. Adult worms pre= dominated in the worm burden from November 1973 to February 1974 and again from November 1974 to January 1975, and fourth stage larvae from March to October 1974.

The peak reached by the faecal worm egg counts during April 1974 was followed by a steady decline until August, after which the numbers rose to reach another peak in December.

*Ostertagia circumcincta*: This nematode was first encountered in lambs slaughtered during January 1974 and thereafter in every lamb slaughtered. Peak burdens exceeding 100 worms were recovered during March and April 1974 and January 1975. Adult worms predominated from January to March 1974 and from October 1974 to January 1975 and fourth stage larvae from April to September 1974.

Larvae were recovered from faecal cultures from January to October 1974. Peak egg counts were recorded during January.

TABLE 11 Survey 5. The mean worm burdens of groups of three tracer lambs slaughtered on dry-land pasture near Tonteldoos on the Transvaal Highveld from August 1973 until January 1975

| Date slaughtered | Mean numbers of worms recovered | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Haemonchus contortus* | | *Ostertagia circumcincta* | | *Trichostrongylus* spp. | | | | *Cooperia* spp. | | | *Trichuris* spp. | *Moniezia expansa* |
| | 4th | Adult | 4th | Adult | 4th | *T. axei* | *T. colubriformis* | *T. rugatus* | 4th | *C. pectinata* | *C. punctata* | Total | Scolices |
| 1973 | | | | | | | | | | | | | |
| 22 May* | 0 | 9 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 1 | 6 | 0 |
| 24 Aug. | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 26 | 0 |
| 21 Sep. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 149 | 0 |
| 19 Oct. | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 46 | 3 |
| 16 Nov. | 1 | 22 | 0 | 0 | 1 | 18 | 2 | 6 | 0 | 8 | 1 | 5 | 8 |
| 14 Dec. | 5 | 26 | 0 | 0 | 0 | 3 | 0 | 16 | 1 | 1 | 1 | 9 | 2 |
| 1974 | | | | | | | | | | | | | |
| 14 Jan.** | 34 | 199 | 2 | 11 | 4 | 0 | 2 | 22 | 3 | 14 | 4 | 3 | 6 |
| 8 Feb. | 696 | 920 | 9 | 39 | 6 | 7 | 40 | 4 | 5 | 26 | 19 | 3 | 50 |
| 7 Mar. | 1 428 | 1 293 | 43 | 58 | 25 | 47 | 163 | 53 | 28 | 67 | 3 | 8 | 10 |
| 5 Apr. | 2 846 | 1 835 | 113 | 57 | 4 | 68 | 94 | 38 | 24 | 9 | 7 | 10 | 7 |
| 3 May** | 392 | 21 | 38 | 20 | 38 | 28 | 25 | 45 | 44 | 12 | 9 | 5 | 1 |
| 30 May | 119 | 9 | 40 | 47 | 6 | 18 | 63 | 138 | 0 | 0 | 2 | 9 | 1 |
| 28 Jun. | 87 | 1 | 38 | 2 | 12 | 23 | 51 | 109 | 1 | 1 | 0 | 7 | 1 |
| 9 Aug.** | 27 | 3 | 36 | 4 | 0 | 3 | 10 | 71 | 1 | 0 | 0 | 7 | 0 |
| 6 Sep.*** | 36 | 2 | 52 | 13 | 0 | 3 | 11 | 10 | 0 | 1 | 0 | 1 | 0 |
| 23 Sep.** | 60 | 8 | 42 | 13 | 1 | 2 | 2 | 9 | 0 | 0 | 0 | 5 | 1 |
| 21 Oct. | 25 | 14 | 10 | 43 | 1 | 0 | 2 | 1 | 0 | 1 | 0 | 9 | 6 |
| 18 Nov. | 0 | 86 | 1 | 43 | 6 | 54 | 0 | 4 | 37 | 43 | 7 | 10 | 3 |
| 17 Dec.** | 5 | 48 | 0 | 9 | 6 | 7 | 1 | 12 | 8 | 38 | 16 | 3 | 2 |
| 1975 | | | | | | | | | | | | | |
| 17 Jan. | 64 | 626 | 1 | 107 | 2 | 17 | 4 | 42 | 4 | 34 | 9 | 6 | 3 |

4th = Fourth stage larvae

* Two flock lambs

** Two tracer lambs only available for slaughter

***One tracer lamb only available for slaughter

TABLE 12 Survey 5. The percentage of *Haemonchus contortus* and *Ostertagia circumcincta* present as fourth stage larvae in tracer lambs slaughtered on dry-land pasture near Tonteldoos on the Transvaal Highveld between November 1973 and January 1975

| Month | No. of sheep slaughtered | Mean worm burdens | | | |
|---|---|---|---|---|---|
| | | *H. contortus* | | *O. circumcincta* | |
| | | Total | % 4th stage | Total | % 4th stage |
| 1973 | | | | | |
| Nov. | 3 | 23 | 4,3 | 0 | - |
| Dec. | 3 | 31 | 16,1 | 0 | - |
| 1974 | | | | | |
| Jan. | 2 | 233 | 14,6 | 13 | 15,4 |
| Feb. | 3 | 1616 | 43,1 | 48 | 18,8 |
| Mar. | 3 | 2721 | 52,5 | 101 | 42,6 |
| Apr. | 3 | 4681 | 60,8 | 170 | 66,5 |
| May | 5 | 242 | 94,4 | 75 | 51,9 |
| Jun. | 3 | 88 | 98,9 | 40 | 95,0 |
| Jul. | - | - | - | - | - |
| Aug. | 2 | 30 | 90,0 | 40 | 90,0 |
| Sep. | 3 | 58 | 89,1 | 58 | 77,1 |
| Oct. | 3 | 39 | 64,1 | 53 | 18,9 |
| Nov. | 3 | 86 | 0,0 | 44 | 2,3 |
| Dec. | 2 | 53 | 9,4 | 9 | 0,0 |
| 1975 | | | | | |
| Jan. | 3 | 690 | 9,3 | 108 | 0,9 |

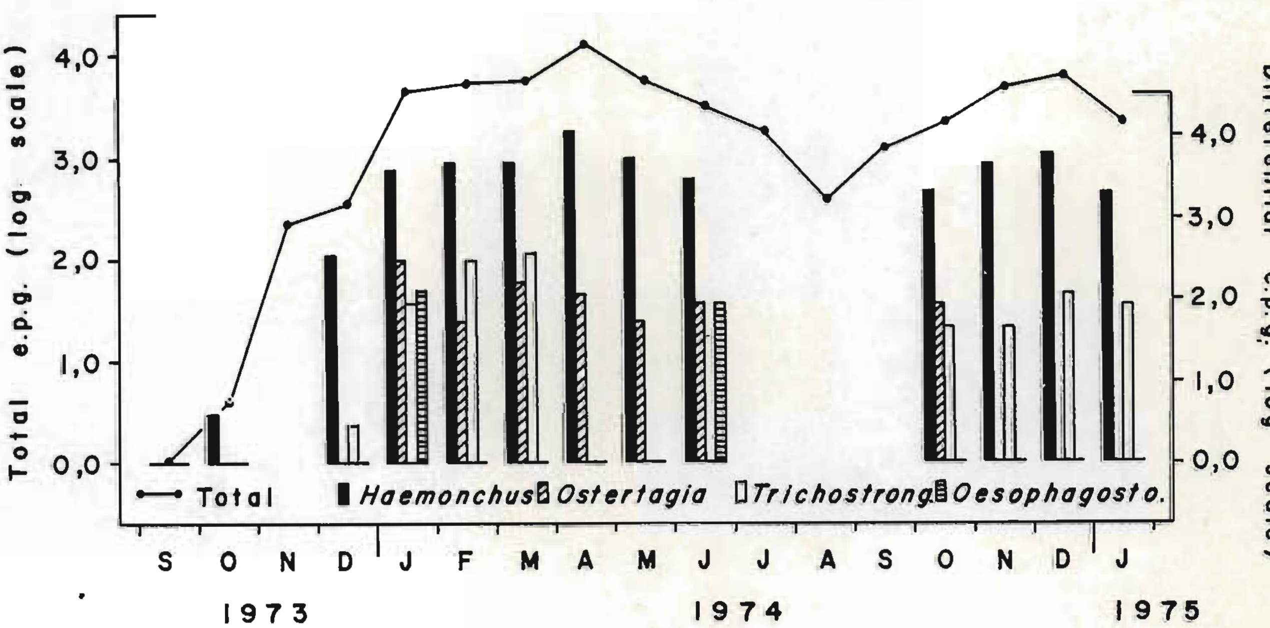



Fig. 6 Survey 5. Total and differential faecal worm egg counts (e.p.g.) of untreated flock lambs on dry-land pasture near Tonteldoos on the Transvaal Highveld. Differential counts were not done in November 1973 and from July to September 1974

*Trichostrongylus* spp.: The three species of this nematode recovered were *T. axei*, *T. colubriformis* and *T. rugatus*. Burdens rose erratically from November 1973 to reach a peak from March to June 1974 and declined thereafter to a low level during October.

*Cooperia* spp.: *C. pectinata* and *C. punctata* were recovered, the former species being more numerous than the latter although both were recovered in small numbers only. No *Cooperia* spp. larvae were recovered from faecal cultures made from the flock lambs.

*Trichuris* spp.: *T. globulosa* and *T. ovis* were recovered erratically throughout the survey period. The largest numbers were encountered during September 1973 when the lambs were confined to a small paddock planted with Kikuyu grass.

Other nematode genera: *Nematodirus spathiger*, *Strongyloides papillosus*, *Oesophagostomum columbianum* and *Skrjabinema* spp. were recovered in small numbers from individual sheep.

*Moniezia expansa*: This cestode was present in practically every lamb slaughtered from October 1973 to April 1974 and from October 1974 until the conclusion of the survey in January 1975. Of 13 lambs slaughtered between May and September 1974, the only four found to be infested harboured one worm each.

*Avitellina* sp.: Two of three lambs slaughtered during February 1974, all three lambs examined during September of the same year, and one lamb slaughtered during January 1975 were infested. No other lambs were infested.

## Discussion

The chief difference between the surveys conducted at Hennops River and the present one is that, whereas the former surveys were conducted so that man-induced interference would wherever possible assist helminth acquisition, the sheep in this survey were subjected to normal husbandry practices, dictated by weaning and seasonal availability of grazing which were not modified because of their possible effect on helminth acquisition.

The most striking effects of these husbandry practices were evident in tracer lambs slaughtered prior to January 1974. The anthelmintic treatment of all flock lambs and their dams during May 1973 and the frequent alteration of paddocks thereafter prevented the build-up of pasture contamination. The eggs of *Trichuris* spp., however, are resistant to adverse conditions (Soulsby, 1965) and probably survived in the Kikuyu paddock after the removal of a previous flock of sheep. Because this paddockwas small and the grazing short, ideal conditions for the acquisition of *Trichuris* spp. infestation were created, as indicated by the worm burdens of the tracer lambs that grazed this paddock during July to September 1973. This phenomenon was not repeated from July to September in the following year, however, when the lambs again grazed this camp.

Despite the fact that the flock lambs had high faecal egg counts from January to May 1974 and had grazed only one paddock during this time, the tracer lambs slaughtered on 3 and 30 May had failed to acquire large infestations. The movement of the flock lambs to fresh pastures during May and July 1974 when faecal egg counts were still fairly high, also failed to result in severe pasture contamination, as judged by the worm burdens of the tracer lambs. This is largely because most of the eggs in the faeces were those of *Haemonchus contortus* and a large proportion of these eggs are apparently unable to develop to the infective stage on pasture in the Transvaal Highveld during the colder months even when supplementary moisture is supplied by irrigation (Surveys 3 and 4).

Despite the fact that the flock lambs had egg counts due to *H. contortus* in excess of 2 000 e.p.g. from October 1974 onwards, the tracer lambs failed to acquire large burdens of this species until January 1975 even though the flock had been grazing the same pasture since the beginning of October 1974. The inability of larvae of *H. contortus* to survive on pasture during spring and early summer is probably due to climatological stresses as suggested by Southcott *et al*. (1976).

Despite irrigation at Hennops River the acquisition of *H. contortus* at Tonteldoos and at Hennops River was similar. It would therefore appear that provided moisture is adequate, temperature and protection from solar radiation are of major importance for the survival of the free-living stages of this species. The earlier protection against solar radiation supplied by the more rapidly growing irrigated pastures at Hennops River and the higher temperature would account for the infestations there from December onward, whereas they were only evident at Tonteldoos from January. Infestations were high until May or June at Hennops River, but only until April at Tonteldoos. This may well be due to the cooler climate and lack of adequate moisture at the latter venue and the poorer protection afforded by the natural pasture.

The pattern of acquisition of *Trichostrongylus* spp. and *Moniezia expansa* at the two localities was almost identical, although irrigation and consequently better pasture cover at Hennops River resulted in higher burdens of both these species. The only *M. expansa* infestations of any note immediately after winter were encountered in the lambs slaughtered during October. The ingestion of mites in which cysticercoids had overwintered would have accounted for these infesta= tions. The level of infestation remained fairly high until April and virtually disappeared during the winter, as development of the cysticercoid in the mite is retarded by cooler temperatures (Kuznetsov, 1970).

Lack of moisture and poor vegetation cover were probably responsible for the fact that the period August to November was unfavourable for the survival or development of the free-living stages of *Haemonchus contortus*, *Ostertagia circumcincta* and *Trichostrongylus* spp. at Tonteldoos.

The availability of *Cooperia* spp. infestation was also largely confined to the period November to May. These nematodes were probably of cattle origin as cattle grazed pastures before or with the sheep.

The development of *Haemonchus contortus*, *Ostertagia circumcincta* and *Cooperia* spp. was arrested in the fourth larval stage during the autumn and winter months. This observation is, however, based on very low worm burdens for the latter two species. The months during which arrested development was present were virtually identical to those for the former two species at Hennops River. At Tonteldoos *Ostertagia circumcincta* exhibited greater inhibition during June and August than at Hennops River. This was probably due to the colder winters in the former district resulting in greater pressure to overwinter as arrested larvae in the host.

The faecal worm egg counts of *Haemonchus contortus* in the flock lambs are corroborative evidence for the hypothesis of overwintering. From October 1973 to April 1974 the counts closely followed the ever-increasing numbers of worms acquired by the tracer lambs. The subsequent drop in egg count is due to both self-cure (Stewart, 1953) and ageing of the adult population as little further infestation was being acquired from the pastures. The sustained rise in egg counts from September to December 1974 cannot be accounted for by any recent acquisition of infestation, as the tracer lambs by that time were picking up very few larvae from the pastures (Table 11), but is due rather to maturation of fourth stage larvae which had been acquired during autumn and winter (Blitz & Gibbs, 1972b).

*Ostertagia circumcincta* had not previously been recovered from sheep on dry-land pastures on the Transvaal Highveld. Thomas (1968) makes no mention of it in his survey in this region, in which he used faecal worm egg counts and cultures as survey tools. The small numbers recovered in the present survey and the low egg-laying capacity of this worm (Gordon, 1933), indicate that it could easily be missed if differential faecal worm egg counts alone are used in surveys.

## *HELMINTHS OF CATTLE*

### Introduction

Many cattle in the Transvaal graze artificially established, irrigated pastures. Many more, however, graze artificial dry-land pastures or natural pastures. The artificially established pastures are found mainly on the Transvaal Highveld, while in the northern Transvaal large herds of beef cattle graze natural pasturage. Helminth infestation may play a role in limiting the productivity of beef or dairy cattle, but in neither of these regions have helminth surveys, based on worm counts at necropsy, been conducted.

Besides cattle, sheep or antelope also make use of the pasturage on many farms and cross-infestation with helminths from one host species to another is an important consideration on such properties.

Survey 6 describes a helminth survey conducted in calves grazed on irrigated pasture in close proximity to the sheep in Survey 3 at Hennops River on the Transvaal Highveld. It affords the opportunity of comparing the worm burdens of the two host speceis and assessing the degree of cross-infestation that took place.

Survey 7 was conducted in cattle grazing natural pastures with impala in the Nylsvley Provincial Nature Reserve in the Boekenhout area of the northern Transvaal. Not only is this survey area situated in an important beef cattle ranching region, but the survey itself was conducted in the same 750 ha area in which Survey 8 had been carried out in impala. The results are thus applicable to a large number of farms in this area and make it possible to assess also the extent of cross-infestation that takes place between cattle and impala.

## *Survey 6. Irrigated pasture. Hennops River*

### Materials and Methods

*Pastures*

The calves were grazed from spring until autumn on a newly-established Kikuyu grass pasture approximately 0,4 ha in size and during winter on an adjacent grass/clover pasture of approximately 0,6 ha.

*Infestation and management*

During January 1969 two ten-month-old Africander oxen, with worm egg counts of 300 to 500 eggs per gram of faeces from naturally acquired infestations of *Haemonchus placei*, *Trichostrongylus* spp., *Cooperia* spp., *Oesophagostomum radiatum* and *Trichuris* spp., were placed in a movable pen enclosing 0,05 ha of pasture. These calves had been borrowed from a neighbouring farm with the intention of infesting the pastures with helminths common to the Hennops River area.

Four days later two five-month-old Friesland-type calves, raised under worm-free conditions, were added to the pen. These calves were to acquire infestation and thereafter serve as a source of contamination of the pasture once the Africander calves had been removed. One of these calves died but the other was left with the Africanders for 3½ months to infest the pasture. Thereafter the Africanders were returned to their owner while the surviving Friesland calf remained on the pasture for a further year as a source of infestation.

For a period of approximately one month before the tracer calves were introduced, the pen with the infested calves was moved every three or four days to an adjacent, previously unused strip of pasture so that the entire Kikuyu pasture could become contaminated. Thereafter the pen was moved only when the enclosed vegetation had been depleted.

On 23 May 1969 the calves were removed from the Kikuyu pasture since it was badly frosted and had stopped growing, and were placed on the adjacent grass/clover pasture, which had previously been grazed by sheep in Survey 3. The calves were reintroduced on to the Kikuyu pasture on 8 October 1969. The grass/clover pasture was grazed by the sheep during October 1969 and thereafter was cut for hay until April 1970 when sheep were grazed for a week; the calves were reintroduced on 11 May 1970 and remained there until the completion of the survey.

Owing to a shortage of grazing the calves were fed lucerne hay in the pen from April to July 1969.

The pastures were irrigated by means of sprinklers, approximately 37,5 mm of water being supplied at intervals of approximately 14 days, and fertilizer was applied when necessary. Rainfall and daily minimum and maximum atmospheric temperatures were recorded.

*Tracer calves*

On 4 February 1969, after the infested animals had been on the Kikuyu pastures for about a month, two worm-free Friesland-type calves approximately five months old, were placed in the pen. However, one of these calves died. This procedure was repeated at monthly intervals whenever calves were available until April 1970. The newly introduced calves were kept on the pasture for two months before slaughter, thus allowing an overlap of one month between successive pairs.

## Results

The worm burdens of the tracer calves are summarized in Table 13.

In all 11 helminth species were recovered from the tracer calves, *Haemonchus* spp. and *Cooperia* spp. being the most numerous.

*Haemonchus* spp.: The adult worms were identified as *H. placei* but the immature worms could have been either this species or *H. contortus* of ovine origin. The calves slaughtered from July to October 1969 and during June 1970, had all grazed pasture previously grazed by sheep infested with *H. contortus* and could therefore have picked up this species. Peak burdens, in excess of 17 000 worms and consisting mainly of early fourth stage larvae, were recovered from the two calves slaughtered during July 1969 and from one calf during June 1970. Adult burdens of over 1 500 worms were recovered from the calf slaughtered during April 1969 and from three of the calves during February and March 1970.

*Ostertagia circumcincta*: Only nine calves were infested with this nematode which was acquired from the pasture previously grazed by the sheep in Survey 3. All the adult worms examined belonged to this species but no specific identification could be made of the fourth stage larvae.

*Trichostrongylus* spp.: Both *T. axei* and *T. colubriformis* were recovered in small numbers, their combined burdens exceeding 1 000 worms in only one of each pair of calves slaughtered during May and October 1969 and June 1970.

*Cooperia* spp.: The level of infestation with *C. pectinata* and *C. punctata* was considerably higher during 1970 than during 1969. During 1969 the highest burdens were recovered from the calves slaughtered during May and July, and from March to June 1970. With the exception of the burdens of the calves slaughtered from October to December 1969, fourth stage larvae rarely accounted for more than one third of the total worm burden.

*Nematodirus spathiger:* This parasite was probably introduced on to the pastures by sheep and was erratically recovered in small numbers throughout the trial period.

TABLE 13 Survey 6. The worm burdens of tracer calves slaughtered on irrigated pasture at Hennops River on the Transvaal Highveld from April 1969 to June 1970

| Date slaughtered | No. of nematodes recovered at necropsy | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Haemonchus* spp. | | *Ostertagia circumcincta* | | *Trichostrongylus* spp. | | *Cooperia* spp. | | *Nematodirus spathiger* | *Oesophagostomum radiatum* | | *Trichuris* spp. |
| | 4th | Adult | 4th | Adult | 4th | Adult | 4th | Adult | Total | 4th | Adult | Total |
| 1969 | | | | | | | | | | | | |
| 13 Apr. | 4 355 | 1 556 | 0 | 0 | 0 | 285 | 0 | 25 | 0 | 1 | 32 | 6 |
| 14 May | 7 860 | 20 | 0 | 0 | 0 | 1 405 | 45 | 309 | 2 | 32 | 45 | 4 |
| 14 May | 4 510 | 54 | 0 | 0 | 0 | 308 | 26 | 230 | 0 | 9 | 38 | 18 |
| 11 Jul. | 18 390 | 95 | 650 | 0 | 0 | 210 | 15 | 422 | 0 | 0 | 0 | 15 |
| 11 Jul. | 17 270 | 0 | 125 | 0 | 0 | 103 | 4 | 126 | 1 | 0 | 3 | 18 |
| 11 Aug. | 7 366 | 86 | 0 | 0 | 0 | 85 | 0 | 147 | 97 | 0 | 2 | 174 |
| 11 Aug. | 7 045 | 83 | 0 | 0 | 0 | 123 | 0 | 89 | 63 | 16 | 1 | 5 |
| 10 Sep. | 2 162 | 2 | 0 | 0 | 0 | 25 | 0 | 28 | 9 | 1 | 3 | 22 |
| 10 Sep. | 2 560 | 8 | 0 | 0 | 20 | 51 | 0 | 22 | 0 | 0 | 1 | 11 |
| 8 Oct. | 244 | 28 | 0 | 0 | 540 | 592 | 12 | 8 | 17 | 10 | 0 | 11 |
| 8 Oct. | 1 107 | 28 | 0 | 0 | 0 | 366 | 1 | 38 | 3 | 4 | 4 | 9 |
| 5 Nov. | 1 107 | 5 | 0 | 0 | 100 | 590 | 33 | 32 | 4 | 0 | 0 | 6 |
| 5 Nov. | 961 | 13 | 0 | 0 | 83 | 241 | 22 | 13 | 6 | 1 | 0 | 4 |
| 3 Dec. | 2 687 | 765 | 0 | 1 | 0 | 11 | 61 | 123 | 35 | 0 | 1 | 6 |
| 3 Dec. | 5 540 | 1 395 | 0 | 0 | 0 | 204 | 154 | 178 | 0 | 0 | 3 | 0 |
| 1970 | | | | | | | | | | | | |
| 8 Jan. | 343 | 183 | 0 | 2 | 0 | 49 | 33 | 186 | 0 | 0 | 0 | 1 |
| 8 Jan. | 802 | 1 025 | 83 | 20 | 15 | 118 | 29 | 325 | 0 | 12 | 5 | 1 |
| 9 Feb. | 2 905 | 1 803 | 0 | 0 | 0 | 124 | 153 | 456 | 0 | 2 | 0 | 5 |
| 9 Feb. | 2 299 | 2 879 | 60 | 105 | 0 | 235 | 345 | 751 | 4 | 0 | 6 | 47 |
| 19 Mar. | 3 260 | 1 803 | 0 | 0 | 4 | 675 | 1 640 | 8 749 | 0 | 1 | 13 | 3 |
| 19 Mar. | 1 750 | 397 | 0 | 0 | 8 | 313 | 495 | 4 545 | 0 | 0 | 0 | 31 |
| 15 Apr. | 195 | 5 | 0 | 0 | 0 | 15 | 195 | 5 423 | 0 | 2 | 0 | 3 |
| 15 Apr. | 1 700 | 176 | 0 | 0 | 0 | 91 | 800 | 2 612 | 0 | 0 | 2 | 8 |
| 14 May | 2 720 | 1 078 | 50 | 0 | 80 | 355 | 6 660 | 19 034 | 15 | 3 | 7 | 15 |
| 12 Jun. | 7 790 | 127 | 0 | 95 | 235 | 975 | 320 | 6 236 | 5 | 0 | 2 | 65 |
| 12 Jun. | 17 130 | 55 | 400 | 0 | 0 | 885 | 490 | 22 215 | 27 | 0 | 7 | 65 |

4th = Fourth stage larvae

*Oesophagostomum radiatum*: The first three calves slaughtered had burdens of over 30 worms, but subsequently burdens were low and four calves harboured no worms at all.

*Trichuris* spp.: Worm burdens of this genus were generally low, the highest individual burdens being recorded during August 1969 and June 1970.

Other helminths: Three calves harboured 28, 26 and 11 adult *Bunostomum phlebotomum* respectively and another three had five, two and four *Moniezia* spp. scolices respectively.

The monthly rainfall, mean minimum and maximum atmospheric temperatures, irrigation and fertilizer applications on the pastures are graphically reproduced in Fig. 7.

Peak atmospheric temperatures were recorded from November 1969 to January 1970, and the lowest during June to August 1969 and May and June 1970. The amount of water supplied to the pasture by irrigation never fell below a monthly total of 75 mm.

The mean monthly totals and percentages of fourth stage larvae of *Haemonchus* spp. recovered from the tracer calves, and of *H. contortus* recovered from the tracer lambs in Surveys 3 and 4 grazing the pastures at Hennops River, are summarized in Table 14.

Peak total burdens exceeding 7 000 worms were recorded in calves slaughtered from June to August, while burdens of fewer than 2 000 worms were recovered from calves slaughtered during January, October and November. More than 90 % of the worms were in the fourth larval stage in calves slaughtered from May to November.

Peak total burdens exceeding 3 800 worms were recovered from tracer lambs during April and May, while burdens of fewer than 1 000 worms were recorded during January and from June to December. From April to July more than 90 % of the worms were fourth stage larvae.

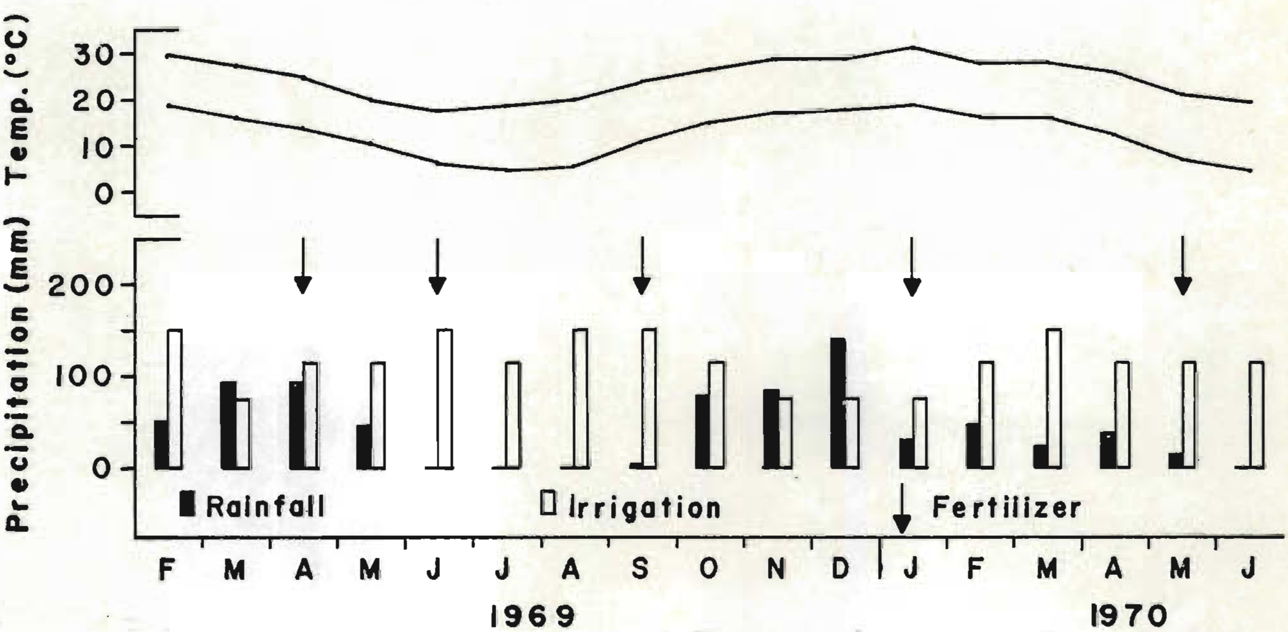



Fig. 7 Survey 6. Atmospheric temperature, rainfall, irrigation and fertilizer applications on the pastures at Hennops River on the Transvaal Highveld between February 1969 and June 1970

TABLE 14 Survey 6. The mean monthly *Haemonchus* spp. burdens of tracer calves and lambs on irrigated pasture at Hennops River on the Transvaal Highveld

| Month slaugh= tered | Calves | | | Lambs | | |
|---|---|---|---|---|---|---|
| | Total No. slaugh= tered | *Haemonchus* spp. recovered | | Total No. slaugh= tered | *H. contortus* recovered | |
| | | Mean total | % 4th stage | | Mean total | % 4th stage |
| Jan. | 2 | 1 177 | 48,7 | 9 | 696 | 43,8 |
| Feb. | 2 | 4 943 | 52,6 | 10 | 1 168 | 65,2 |
| Mar. | 2 | 3 605 | 69,5 | 10 | 1 003 | 61,6 |
| Apr. | 3 | 2 662 | 78,3 | 13 | 3 840 | 92,5 |
| May | 3 | 5 414 | 92,9 | 13 | 4 127 | 92,9 |
| Jun. | 2 | 12 551 | 99,3 | 10 | 720 | 95,6 |
| Jul. | 2 | 17 878 | 99,7 | 10 | 198 | 92,1 |
| Aug. | 2 | 7 290 | 98,8 | 8 | 238 | 82,6 |
| Sep. | 2 | 2 366 | 99,8 | 8 | 33 | 60,8 |
| Oct. | 2 | 704 | 96,0 | 10 | 32 | 75,2 |
| Nov. | 2 | 1 043 | 99,1 | 13 | 137 | 10,1 |
| Dec. | 2 | 5 194 | 79,2 | 13 | 462 | 36,6 |

## Discussion

In Surveys 3 and 4 conducted in sheep at Hennops River a high degree of arrested development of *H. contortus* from April to July was a striking feature. In the present survey in cattle a similar percentage of *Haemonchus* spp. failed to develop to maturity from May to November.

In the former surveys tracer sheep were exposed to infestation for periods of only 33 days and it was felt that immunity induced by continuous exposure was unlikely to have caused any retardation of larval development. In the present survey tracer calves were allowed to graze for two months and the continuous ingestion of larvae may have stimulated an immune response, resulting in retarded larval development, as noted by Roberts (1957) who artificially infested calves each day with the larvae of *H. placei*. From May to November inhibition was virtually complete, irrespective of whether calves harboured burdens of 272 or 18 485 worms, whereas during December to April some worms developed to adulthood whether total burdens consisted of 200 or 6 935 worms. This seasonal occurrence of arrested larval development largely discounts the possibility that immunity, which should act independently of season, was the sole inhibiting factor, though it was probably partially responsible for the generally high degree of inhibition encountered in all calves throughout the survey.

It could be argued that the accumulation of fourth stage larvae in calves slaughtered during July 1969 and June 1970 was partly due to ingestion of *H. contortus* larvae on the pastures previously grazed by sheep and failure of this parasite to develop to adulthood in calves. The calves slaughtered in May 1969, however, had grazed on the Kikuyu pastures which were contaminated with *H. placei* only and these larvae also failed to develop into adults.

The calves were slaughtered 48h after their removal from the pasture, thus many recently ingested third stage larvae had time to develop to the fourth stage (Bremner, 1956). In this way the large burdens of immature worms could have been recently acquired. This, however, would not explain why the vast majority of larvae was still in the fourth stage after a two-month grazing period.

Irrespective of the above possibilities it is obvious that from May to November development of *Haemonchus* spp. beyond the fourth larval stage was virtually completely arrested and that this nematode probably overwinters in the host animal in this state.

This finding coincides with those arrived at for *Ostertagia ostertagi* by Anderson, Armour, Jennings, Ritchie & Urquhart (1969) in Scotland, and for *Cooperia oncophora* by Michel, Lancaster & Hong (1970b) in England and Smith (1974) in Canada. The development of these helminths becomes arrested in the host in order to survive severe winters, whereas *Haemonchus placei*, a parasite of cattle in milder climates, uses the same method to survive comparatively mild winters.

The trigger mechanism for this inhibition could be environmental stimuli such as chilling, acting on the infective larvae (Armour & Bruce, 1974). It has been suggested by Waller & Thomas (1975), however, that environmental stimuli such as declining autumn temperatures, are not necessarily a stimulus for subsequent inhibition of development in *H. contortus* and that it may be due to adaptation of the parasite to the particular environment in which it finds itself.

The acquisition of *Haemonchus* spp. infestation from the pastures at Hennops River differed markedly between tracer calves and tracer lambs, particularly during the winter. The calves slaughtered during July and August harboured mean burdens of more than 7 000 worms whereas the lambs examined during the same months had mean burdens below 250 (Table 14). This difference in ability to survive on the pastures during winter indicates that the calves were infested with *H. placei* and the lambs with *H. contortus* and/or that the cattle dungpat is a more effective reservoir of larvae during the winter (Durie, 1962) than the faecal pellets of sheep.

The period of arrested larval development in the two host species also differed. In the calves more than 90 % of the *Haemonchus* spp. burdens consisted of fourth stage larvae from May to November, whereas this occurred in the lambs from April to July (Table 14).

These marked differences lead one to believe that the cattle were infested with *H. placei* and the sheep with *H. contortus* and that little cross-infestation took place. This assumption is confirmed by Roberts

(1942) who showed that cattle are poor hosts of *H. contortus* and by Southcott & Barger (1975) who showed that they can even be used to decontaminate pastures previously contaminated by sheep harbouring this parasite. Consequently I will henceforth refer to the parasites recovered from tracer calves at Hennops River as *H. placei*.

These findings suggest that the generation interval (i.e. adult to adult) of *H. placei* in cattle at Hennops River is considerably longer than that of *H. contortus* in sheep. Marked inhibition of development was present for seven months of the year in the former helminth compared with only four months in the latter. This observation appears to be anomalous because, judging by the large numbers of larvae acquired from the pastures during winter, larvae of *H. placei* can apparently survive on pastures during these months better than can those of ovine origin (Table 14). Yet this parasite undergoes a longer period of larval inhibition in calves in order to survive in the host rather than on the pastures.

The survival of the free-living stages of *H. placei* during winter is in agreement with the findings of Reinecke (1960b). He found that, during winter in the north-western Cape Province, larvae of *H. placei* could develop to the infective stage in the dungpat, albeit in reduced numbers, and that adequate moisture in the dungpat, which acted as a larval reservoir, was essential for their survival. Irrigation of the pastures at Hennops River would have supplied the necessary moisture for larger numbers of preinfective larvae to develop to the infective stage as well as wetting the crust of the dungpat, thus allowing infective larvae to migrate from the dung on to the herbage (Roberts, O'Sullivan & Riek, 1952; Reinecke, 1960a).

The increased numbers of adult *H. placei* recovered from calves slaughtered from December to April also agree with the finding of Reinecke (1960b). The increases due to *H. placei* he recorded in faecal worm egg counts from December onwards reached peaks in autumn. The large larval burdens present in calves slaughtered during autumn and winter confirm observations made in Queensland by Durie (1962), that the larvae of *H. placei* were most abundant on a calf pasture during late summer and winter.

Arrested development of *Cooperia* spp. was not evident in this survey.

At Wallaceville in New Zealand, where winters are colder than at Hennops River, Brunsdon (1972) recorded varying degrees of retardation in the fourth larval stage from May to September. In Canada, where winters are even colder than those at Wallaceville, New Zealand, Smith (1974) found that retardation of *C. oncophora* in the fourth larval stage was virtually complete in calves slaughtered during late autumn. It would thus appear that the degree of larval inhibition and time of its onset is dictated by the severity of the cold period during autumn and winter and consequently by its effect on the survival of the free-living stages. Thus the colder this period and hence the poorer the chances of survival of the free-living stages, the greater the percentage of *Cooperia* spp. that will be arrested in their development.

The peak adult *Cooperia* spp. worm burdens recovered from March to June coincide with the seasonal incidence of this parasite as described in the north-western Cape Province by Reinecke (1960b). In Queensland Durie (1962) estimated the daily ingestion of larvae of *Cooperia* spp. by calves to be greatest during June, July and December.

In Surveys 3 and 4 conducted in sheep at Hennops River, *Oesophagostomum columbianum* was introduced on to the pastures by infested sheep during 1968, but the infestation took a long time to become established and it was only during 1972 and 1973 that fairly large numbers of worms were recovered from tracer lambs. A similar pattern was noted in *O. radiatum* in the present survey; the first three calves slaughtered had fairly reasonable worm burdens but thereafter infestation was erratic and burdens were small. It is, however, possibe that when the infested Africander calves were returned to their owner during May 1969, a major source of pasture contamination was removed before the Friesland calf had become heavily infested and itself a major source of infestation on the pasture.

The recovery from tracer calves of *Ostertagia circumcincta* and *Nematodirus spathiger*, which are normally regarded as nematode parasites of sheep, indicates that calves can acquire infestations with these species. Southcott & Barger (1975) found that sheep pastures had to be grazed by cattle for 12 weeks to reduce *Ostertagia circumcincta* contamination and for 24 weeks to reduce contamination with *Nematodirus spathiger*, thus indicating a fairly long period of survival in the bovine host.

## *Survey 7. Natural Pasture. Boekenhout*

### Materials and Methods

*Pastures*

The survey area of 750 ha of grazing was divided by wire fences into four unequal camps. For decades cattle had grazed this particular area for a limited period from mid-January to mid-May, because the poisonous plant *Dichapetalum cymosym* (gifblaar) is rarely eaten during these months. At other times it is either more abundant or more attractive to the animals because grass cover is inadequate, and no cattle were allowed to graze during these times, because experience had shown that many cattle had died of gifblaar poisoning.

*Infestation*

As was the custom in the past approximately 200 ten- to 12-month-old cattle were brought into the camps during January 1976. Approximately half of these animals were not treated with an anthelmintic while grazing these camps, while half of the remainder were treated once and the other half regularly at intervals of two weeks. This treatment regime was followed because these cattle were utilized in a production trial assessing the effect of helminth infestation on live mass gain.
Apart from 14 animals which were to serve as a source of infestation and as tracer animals all cattle were removed during the first week of May 1976.

From May 1976 until February 1977 a group of at least eight untreated cattle, of which six were present for the duration of the survey, grazed the survey area and served as a source of pasture contamination.
During January 1977 250 eight- to ten-month-old calves from neighbouring farms were introduced into the study area and remained there until the completion of the survey.

*Tracer cattle*

Twenty-four oxen were used to monitor infestation in the study area; 16 were selected from the 200 animals which had originally grazed this area, while the other eight came from an adjacent farm.

The oxen were divided into pairs and each pair was drenched with parbendazole at approximately 80 mg/kg live mass four weeks prior to slaughter to remove existing nematode burdens. The animals slaughtered during August 1976 and January 1977, however, were drenched six weeks before slaughter. Only one animal of the pair was slaughtered during August as the other had escaped and could not be found for two weeks. Slaughtering was so arranged that two animals were culled during each calendar month of the survey.

*General*

At approximately 14-day intervals faeces for faecal worm egg counts were collected from the same six cattle which served as a source of infestation throughout the survey. After the counts had been completed the faeces were mixed and a single faecal culture was made for larval differentiation.

Minimum and maximum atmospheric temperatures and rainfall were recorded daily in the survey area.

## Results

The total worm burdens of the animals are summarized in Table 15, while the monthly mean burdens of the major genera and the percentage of *Haemonchus placei* and *Cooperia* spp. in the fourth larval stage are summarized in Table 16.

Nine nematode species, one trematode and one cestode were recovered from the tracer cattle. *Haemonchus placei* and *Cooperia* spp. were the most abundant parasites, while all the animals were infested with *Oesophagostomum radiatum*.

*Haemonchus placei*: Worms of this species were recovered from every animal slaughtered from March to July and from November to February and peak total burdens exceeding 900 worms were recorded during December and January. Not a single animal was infested from August to October. Adult worms outnumbered fourth stage larvae from November to January, but from March to July 1976 and in February 1977 more than 60 % of the total burden consisted of fourth stage larvae. Peak egg counts were recorded from November 1976 to February 1977.

TABLE 15 Survey 7. The total nematode burdens of tracer cattle slaughtered on natural pasture near Boekenhout in the northern Transvaal between March 1976 and February 1977

| Animal No. | Date slaughtered | Number of helminths recovered | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *Haemonchus placei* | | *Longistrongylus sabie* | | *Trichostrongylus* spp. | | | *Cooperia* spp. | | | *Impalaia tuberculata* | | *Oesophagostomum radiatum* | | | | |
| | | 4th | Adult | 4th | Adult | 4th | *T. colubriformis* | *T. falculatus* | 4th | *C. pectinata* | *C. punctata* | 4th | Adult | 4th | Adult | | | |
| | 1976 | | | | | | | | | | | | | | | | | |
| 1 | 11 Mar. | 56 | 25 | 10 | 50 | 0 | 60 | 90 | 500 | 50 | 0 | 225 | 0 | 3 | 5 | | | |
| 2 | 11 Mar. | 732 | 75 | 72 | 28 | 100 | 100 | 101 | 541 | 75 | 50 | 350 | 0 | 0 | 5 | | | |
| 3 | 8 Apr. | 644 | 0 | 0 | 0 | 50 | 0 | 75 | 1 734 | 656 | 884 | 165 | 0 | 3 | 0 | | | |
| 4 | 8 Apr. | 475 | 0 | 0 | 1 | 0 | 0 | 0 | 1 181 | 725 | 578 | 50 | 0 | 5 | 5 | | | |
| 5 | 6 May | 477 | 0 | 0 | 0 | 0 | 77 | 6 | 1 171 | 306 | 456 | 0 | 0 | 3 | 6 | | | |
| 6 | 6 May | 275 | 0 | 1 | 0 | 0 | 6 | 0 | 203 | 110 | 124 | 0 | 0 | 3 | 3 | | | |
| 7 | 3 Jun. | 520 | 0 | 0 | 0 | 275 | 0 | 225 | 1 800 | 425 | 450 | 1 103 | 0 | 79 | 13 | | | |
| 8 | 3 Jun. | 576 | 0 | 50 | 0 | 0 | 0 | 0 | 1 578 | 225 | 278 | 0 | 0 | 0 | 10 | | | |
| 9 | 2 Jul. | 205 | 0 | 0 | 0 | 0 | 0 | 0 | 775 | 0 | 150 | 0 | 0 | 0 | 5 | | | |
| 10 | 2 Jul. | 175 | 0 | 0 | 0 | 0 | 0 | 0 | 250 | 1 | 50 | 0 | 0 | 100 | 20 | | | |
| 11* | 12 Aug. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 0 | 25 | 0 | 160 | 199 | | | |
| 12 | 9 Sep. | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 31 | 13 | | | |
| 13 | 9 Sep. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 109 | 5 | | | |
| 14 | 7 Oct. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 56 | 1 | | | |
| 15 | 7 Oct. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 26 | 14 | | | |
| 16 | 4 Nov. | 0 | 50 | 1 | 0 | 50 | 125 | 0 | 250 | 325 | 50 | 250 | 0 | 25 | 20 | | | |
| 17 | 4 Nov. | 50 | 200 | 0 | 0 | 100 | 282 | 81 | 225 | 400 | 50 | 25 | 0 | 75 | 3 | | | |
| 18 | 1 Dec. | 425 | 500 | 0 | 0 | 325 | 901 | 225 | 1 225 | 900 | 700 | 0 | 25 | 125 | 5 | | | |
| 19 | 1 Dec. | 775 | 1 100 | 450 | 75 | 200 | 3 137 | 425 | 1 625 | 1 434 | 425 | 1 100 | 1 675 | 125 | 3 | | | |
| | 1977 | | | | | | | | | | | | | | | | | |
| 20* | 13 Jan. | 275 | 1 200 | 4 | 28 | 0 | 603 | 0 | 100 | 125 | 525 | 0 | 0 | 105 | 150 | | | |
| 21* | 13 Jan. | 225 | 729 | 0 | 0 | 0 | 0 | 0 | 50 | 150 | 125 | 0 | 0 | 67 | 78 | | | |
| 22 | 11 Feb. | 457 | 225 | 0 | 0 | 0 | 0 | 0 | 275 | 106 | 53 | 0 | 0 | 5 | 23 | | | |
| 23 | 11 Feb. | 175 | 150 | 0 | 0 | 25 | 3 | 0 | 153 | 0 | 0 | 0 | 0 | 0 | 10 | | | |

A single animal was slaughtered on 12 August

* Exposed for 6 weeks

TABLE 16 Survey 7. The monthly mean total burdens of the dominant helminth species and the percentage fourth stage larvae of *Haemonchus placei* and *Cooperia* spp. in tracer cattle grazed on natural pasture near Boekenhout in the northern Transvaal between March 1976 and February 1977

| Month | Mean worm burdens | | | | | |
|---|---|---|---|---|---|---|
| | *Haemonchus placei* | | *Tricho= strongylus* spp. | *Cooperia* spp. | | *Oesophago= stomum radiatum* |
| | Total | % 4th | Total | Total | % 4th | Total |
| 1976 | | | | | | |
| Mar. | 444 | 88,7 | 226 | 608 | 85,6 | 7 |
| Apr. | 560 | 100,0 | 63 | 2 879 | 50,6 | 7 |
| May | 376 | 100,0 | 45 | 1 185 | 58,0 | 8 |
| Jun. | 548 | 100,0 | 250 | 2 378 | 71,0 | 51 |
| Jul. | 190 | 100,0 | 0 | 613 | 83,6 | 63 |
| Aug.* | 0 | - | 0 | 25 | 100,0 | 368 |
| Sep. | 0 | - | 3 | 0 | - | 79 |
| Oct. | 0 | - | 0 | 0 | - | 49 |
| Nov. | 150 | 16,6 | 319 | 650 | 36,5 | 62 |
| Dec. | 1 400 | 42,9 | 2 607 | 3 155 | 45,2 | 129 |
| 1977 | | | | | | |
| Jan.* | 1 215 | 20,6 | 302 | 538 | 14,0 | 200 |
| Feb. | 504 | 62,8 | 14 | 294 | 72,9 | 19 |

4th = Fourth stage larvae

* Exposed for 6 weeks

*Longistrongylus sabie:* This nematode was recovered in small numbers from individual animals from March to June and from November to January. Peak mean burdens occurred during March and December.

*Trichostrongylus* spp.: *T. colubriformis* and *T. falculatus* were recovered and two animals also harboured *T. axei*. The spicules of the *T. colubriformis* recovered had very short hooks and the spicule immediately anterior to the hook was markedly concave when compared with the fairly long hook and slight concavity of the spicules normally encountered in this species (see pp. 12 and 13). Every animal slaughtered during March, May, November and December was infested with worms of this genus and peak burdens exceeding 1 400 worms were recorded during December. Peak egg counts were recorded in June 1976 and during January and February 1977.

*Cooperia* spp.: Both *C. pectinata* and *C. punctata* were present and every animal slaughtered from March to August and from November to February was infested. Peak total burdens exceeded 1 900 worms in individual animals from April to June and in December, adults out= numbering fourth stage larvae from November to January. The proportion of fourth stage larvae increased from 50 % in April to 100 % during August. Large percentages of fourth stage larvae were, however, also encountered during March and February. Peak egg counts were recorded during May 1976.

*Impalaia tuberculata*: Ten animals harboured this nematode, every animal examined during March, April, August, November and December was infested. Fourth stage larvae were present in nine calves and adult worms were recovered from only two animals. Infective larvae were recovered only from faecal cultures made during February 1976 before the first animals were slaughtered and from no other cultures.

*Oesophagostomum radiatum*: This helminth was recovered from every animal, and mean burdens exceeded 50 worms from June to January. Peak egg counts were recorded during September and October 1976.

General: One animal harboured one *Moniezia benedeni*. Although the rumens of nine cattle contained adult paramphistomes, no worms were recovered from the lungs, livers or oesophagi of any of the animals. The carcass of one animal exhibited lesions typical of *Parafilaria bovicola* infestation, but no worms were recovered.

The monthly mean total and differentiated faecal worm egg counts of the cattle which served as a source of infestation, and the atmospheric temperature and rainfall in the survey area are graphically represented in Fig. 8.

The highest maximum temperatures were recorded in the survey area from November 1976 to February 1977, and the lowest minimum temperatures during June and July 1976. No rain fell from June to August.

## Discussion

The results of this survey can be compared with those obtained in Survey 6 in calves on irrigated, artificially established pastures at Hennops River. In Survey 6, *Haemonchus placei* was recovered throughout the year. The peak burdens recorded in the calves slaughtered during July were followed by a progressive decrease until October and then by a rise to a minor peak in December. In the present survey the burdens of *H. placei* followed a basically similar pattern, except that in this case the major peak was reached during December and January while the minor peak occurred from April to June, and no worms were present from August to October.

At Hennops River the greatest number of *Trichostrongylus* spp. was recorded during June while the worm burdens from July to September were low. At Boekenhout the largest burdens were recovered from cattle during December while few or no worms were present from July to October. In sheep this nematode is usually present in larger numbers during the cooler months of the year (Reinecke, 1964; Muller, 1968; Viljoen, 1969), but the extremely dry conditions prevailing at Boekenhout during these months must have contributed to the disappearance of infective larvae from the pastures. Similar observations have been made in sheep during a dry winter at Outeniqua in the Cape Province (Snijders *et al.*, 1971). In the Karoo, however, Viljoen (1969) recovered the greatest numbers of *T. falculatus* from tracer lambs during the autumn and winter months despite the virtual absence of rain. He concluded that when the monthly mean temperature exceeded 20$^{o}$C, rainfall, even if it exceeded 50 mm a month, resulted in only a very slight increase in *T. falculatus* burdens. In the present survey monthly mean temperatures exceeded 20$^{o}$C during November and December and yet the

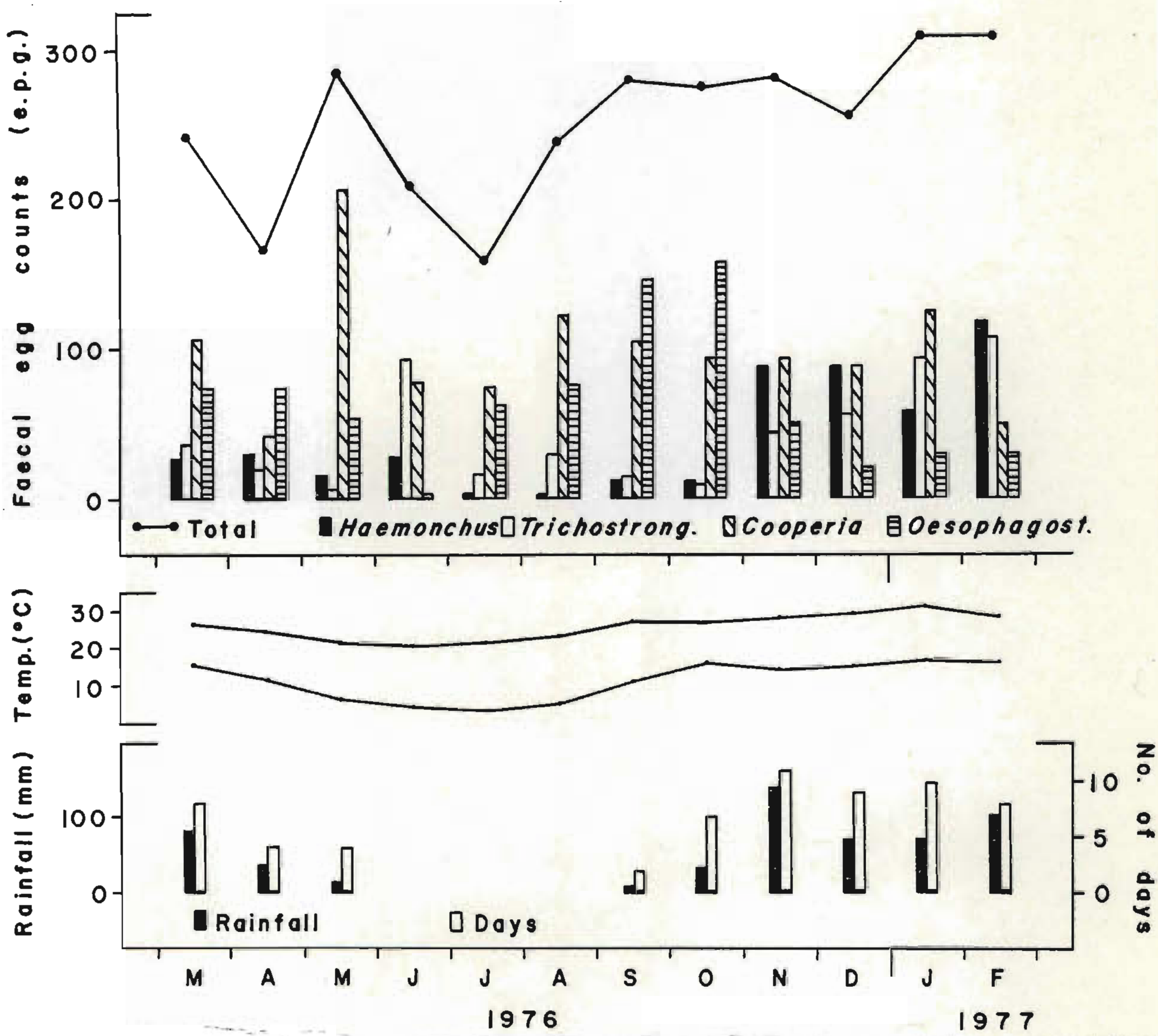



Fig. 8 Survey 7. Total and differential faecal worm egg counts (e.p.g.) of infested cattle, atmospheric temperature, rainfall and number of days on which rain fell on natural pastures near Boekenhout in the northern Transvaal between March 1976 and February 1977

largest *T. colubriformis* and *T. falculatus* burdens were recovered from cattle slaughtered during December.

In the cattle at Hennops River, peak *Cooperia* spp. burdens were present during May and June and comparatively low numbers from August to January. At Boekenhout, the peak numbers present from April to June were followed by the complete absence of parasites during September and October and then by a major peak in December.

In the present survey arrested development of *Haemonchus placei* in the fourth larval stage was marked from March to July. This inhibition of development was present in *H. contortus* in sheep from April or May until July or August in Surveys 3, 4 and 5 and in *H. placei* in calves from May to November in Survey 6.

*Haemonchus* spp. were recovered throughout the year from animals slaughtered in Surveys 3 to 6, indicating that their survival on the pastures was possible during all seasons. Near Boekenhout, however, since no *H. placei* were recovered from cattle slaughtered during August to October, it must be assumed that there were no infective larvae on the pasture during these months. Inhibition of development in the host during the preceding months, when larvae were still available on the pasture, was therefore a very real necessity to bridge this period in order to survive.

The greatest numbers of *Oesophagostomum radiatum* were recovered from calves slaughtered from June to January. It seems remarkable that this parasite could survive on the pastures from August to October, when climatic conditions were particularly unfavourable for the acquisition of all other helminths. In a study on the epizootiology of helminth infestation in calves in the north-western Cape Province, Reinecke (1960b) found that egg counts of *O. radiatum* reached their maximum during winter and that at necropsy this species was more plentiful during winter than at any other time. He suggested, however, that these calves had become infested during the summer and autumn, a theory which was not confirmed by the present findings.

Gerber (1975) demonstrated that *O. radiatum* can infest calves percuta=neously. It is possible that infestation at Boekenhout survived during the dry months of the year in moist soil round a drinking place in a small marshy area, and that the cattle became infested while standing in this soil. This may account for the presence of this parasite in cattle during those months when all other helminths were at a low level or absent.

The presence in tracer cattle of adult *Longistrongylus sabie* and *Impalaia tuberculata*, parasites normally found in impala (Mönnig, 1924, 1933; Survey 8), indicates that these nematodes can become naturally established in cattle. The generally small number of adult helminths of these species recovered and few cattle infested in the present survey show, however, that cattle are not good alternative hosts for these parasites. Except in one animal, neither of these helminths was recovered from July to October.

The fact that most parasites of nearly all species were recovered during December is possibly the result of the warm weather and abundant rainfall during November. Similar temperatures and rainfall during February 1976, however, did not result in very large worm burdens in the animals slaughtered during March. The high December burdens differ considerably from the seasonal fluctuations in worm burden recorded in calves at Hennops River where the greatest numbers of *Haemonchus placei*, *Trichostrongylus* spp. and *Cooperia* spp. were present during June or July (Survey 6). Irrigation, climate and nature of the artificial pastures at Hennops River probably account for this difference.

The paramphistomes recovered from the rumens of some of the animals had probably been acquired before the animals had been brought into the study area, as no suitable habitat for *Bulinus tropicus* the intermediate snail host, existed in the survey area.

## HELMINTHS OF ANTELOPE

### Introduction

Of the numerous antelopes in South Africa impala and blesbok lend themselves to semi-domestication more easily than most other species. The relative simplicity with which they are captured and confined and the fact that they readily breed in captivity, provided the area in which they are confined is not too small, has led to these buck being kept on many farms.

Several of the nematodes parasitic in impala have been described by Mönnig (1924, 1933) and Ortlepp (1938, 1964b), while Mönnig (1931a, 1932) has also described many nematodes from blesbok and Round (1968) has prepared check-lists of helminths recovered from both species. No studies on seasonal fluctuations of worm burdens in impala or blesbok have as yet been published. With the exception of the surveys of Bindernagel & Todd (1972) in buffalo in Uganda and Baker & Anderson (1975) in white-tailed deer in Canada, few such studies in any antelope species appear to have been reported.

The four surveys reported here describe the fluctuations in worm burdens of impala culled in the Nylsvley Provincial Nature Reserve in the Boekenhout area over a period of 13 months and in blesbok in the Percy Fyfe Provincial Nature Reserve at Lunsklip during a period of 17 months, as well as the prevalence of infestation in 12 impala culled in the Pafuri area of the Kruger National Park and in 28 blesbok shot in the Rob Ferreira Reserve at Badplaas. The blesbok were examined also for the presence of larvae of oestrid flies and the impala at Boekenhout for arthropod parasites. Some of these findings have been reported separately (Horak & Butt, 1977).

## *Survey 8.* *Impala near Boekenhout*

### Materials and Methods

#### *Study area*

The Nylsvley Nature Reserve is situated near Boekenhout in the Naboom= spruit District of the Transvaal. The impala were all culled within the same 750 ha area in this reserve as that in which the cattle in Survey 7 were to graze from February 1976 to February 1977. This area had for many decades been grazed every year from January to May by approximately 200 to 300 cattle.

#### *Helminth collection*

Two to four impala were shot monthly from February 1975 to February 1976. The carcasses were transported to a central point where they were skinned and eviscerated and the ages of the antelope under two years of age estimated on size, taking into consideration that nearly all impala at Nylsvley were born during November. The rumens were immediately opened and the contents and walls examined for paramphistomes. The livers, lungs and gastro-intestinal tracts were placed in plastic bags and transported to the laboratory for further processing, and faeces were collected from the recta for faecal worm egg counts.

*Climatic data*

Minimum and maximum atmospheric temperature and rainfall were recorded in the study area from May 1975 to February 1976.

## Results

The total helminth burdens of each of the impala are presented in Table 17.

Thirteen nematode species, two trematodes and a cestode were recovered.

Because the worm burdens of young animals differed from those of adults the findings for these two age groups were treated separately.

The following trends were observed in the worm burdens of animals aged 12 months and more:

(a) Burdens of adult *Haemonchus placei* in excess of 100 worms were recovered from individual animals during February, March and November and from all animals in October 1975. Fourth stage larvae reached peak levels generally in excess of 400 worms from April to October.

(b) *Longistrongylus sabie* adults generally exceeded 100 worms in February, March, June, November and December and fourth stage larvae 300 worms from May to September.

(c) No clear pattern could be determined for the seasonal incidence of *Trichostrongylus* spp. but burdens below the mean were recovered during March, April and October 1975 and February 1976.

TABLE 17 Survey 8. The total worm burdens of impala culled in the Nylsvley Nature Reserve near Boekenhout in the northern Transvaal from February 1975 to February 1976

| No. and sex | Age (m = Months) | Month culled | Number of helminths recovered | | | | | | | | | | | | | | | | | Other helminths |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *Paramphistomum* sp. | *Haemonchus placei* | | *Longistrongylus sabie* | | *Trichostrongylus* spp. | | | | *Impalaia tuberculata* | | *Cooperia* and *Cooperioides* | | | | *Oesophagostomum columbianum* | | |
| | | | | | | | | | *T. axei* | *T. colubriformis* | *T. falculatus* | | | | *C. hungi* | *C. hamiltoni* | *C. hepaticae* | | | |
| | | | | 4th | Adult | 4th | Adult | 4th | Adult | Adult | Adult | 4th | Adult | 4th | Adult | Adult | Adult | 4th | Adult | |
| | | 1975 | | | | | | | | | | | | | | | | | | |
| 1 M | 3m | Feb. | 0 | 6 | 40 | 0 | 0 | 10 | 0 | 50 | 0 | 20 | 249 | 60 | 256 | 30 | 0 | 0 | 0 | |
| 2 M | 15m | Feb. | 0 | 102 | 250 | 5 | 225 | 0 | 0 | 1 415 | 112 | 1 327 | 4 649 | 281 | 1 403 | 795 | 0 | 0 | 12 | |
| 3 F | Adult | Mar. | 91 | 448 | 187 | 442 | 220 | 40 | 0 | 435 | 267 | 3 362 | 3 859 | 2 640 | 1 122 | 2 611 | 0 | 0 | 23 | |
| 4 F | Adult | Mar. | 68 | 185 | 15 | 471 | 15 | 5 | 16 | 0 | 0 | 2 426 | 0 | 7 333 | 490 | 60 | 2 | 0 | 0 | |
| 5 M | Adult | Mar. | 60 | 96 | 65 | 30 | 155 | 6 | 0 | 901 | 0 | 2 241 | 1 752 | 241 | 1 009 | 800 | 33 | 0 | 12 | 4 *Fasciola gigantica*, 1 *Trichuris* sp. |
| 6 M | 5m | Apr. | 0 | 445 | 200 | 11 | 0 | 0 | 25 | 90 | 20 | 1 856 | 211 | 547 | 219 | 35 | 9 | 0 | 0 | |
| 7 M | 5m | Apr. | 0 | 282 | 0 | 109 | 5 | 30 | 16 | 191 | 80 | 2 129 | 562 | 358 | 212 | 80 | 33 | 0 | 0 | |
| 8 F | Adult | Apr. | 0 | 826 | 50 | 198 | 10 | 5 | 0 | 553 | 163 | 6 107 | 124 | 1 874 | 496 | 624 | 1 | 23 | 2 | 2 *Moniezia expansa* |
| 9 M | Adult | Apr. | 0 | 604 | 20 | 167 | 20 | 0 | 0 | 1 040 | 0 | 7 154 | 3 349 | 1 727 | 1 964 | 240 | 3 | 1 | 35 | 1 *Gongylonema pulchrum* |
| 10 F | 6m | May | 0 | 471 | 25 | 183 | 0 | 30 | 275 | 414 | 80 | 2 095 | 414 | 612 | 354 | 268 | 33 | 0 | 0 | |
| 11 F | Adult | May | 2 | 5 040 | 13 | 1 099 | 1 | 20 | 66 | 1 562 | 0 | 10 354 | 421 | 3 013 | 685 | 2 436 | 1 | 30 | 2 | 3 *Moniezia expansa* |
| 12 F | 7m | Jun. | 0 | 467 | 5 | 81 | 5 | 26 | 130 | 183 | 261 | 3 050 | 131 | 907 | 116 | 73 | 4 | 0 | 0 | 2 *Moniezia expansa* |
| 13 M | Adult | Jun. | 54 | 1 493 | 60 | 307 | 120 | 200 | 293 | 1 670 | 241 | 4 696 | 60 | 1 790 | 140 | 181 | 2 | 0 | 9 | |
| 14 M | Adult | Jun. | 22 | 1 175 | 40 | 551 | 170 | 80 | 161 | 1 723 | 260 | 12 800 | 3 874 | 4 888 | 586 | 972 | 34 | 0 | 6 | |
| 15 F | 20m | Jul. | 18 | 770 | 1 | 519 | 0 | 4 | 0 | 631 | 0 | 9 469 | 0 | 5 165 | 10 | 200 | 0 | 10 | 1 | |
| 16 F | Adult | Jul. | 31 | 600 | 10 | 1 135 | 0 | 0 | 0 | 0 | 0 | 1 947 | 0 | 3 748 | 20 | 343 | 5 | 20 | 0 | |
| 17 F | Adult | Jul. | 16 | 1 490 | 10 | 8 586 | 0 | 80 | 60 | 2 600 | 0 | 9 354 | 0 | 11 868 | 110 | 0 | 2 | 0 | 6 | 3 *Gongylonema pulchrum*, 1 *Moniezia expansa* |
| 18 M | Adult | Jul. | 37 | 1 777 | 20 | 577 | 10 | 164 | 361 | 3 040 | 180 | 18 285 | 3 740 | 3 665 | 885 | 1 300 | 492 | 30 | 26 | 1 *Moniezia expansa* |
| 19 M | Adult | Aug. | 0 | 645 | 0 | 683 | 0 | 1 | 518 | 1 020 | 0 | 16 780 | 40 | 6 285 | 0 | 715 | 37 | 40 | 19 | |
| 20 M | Adult | Aug. | 17 | 833 | 0 | 393 | 1 | 40 | 0 | 1 265 | 10 | 13 360 | 535 | 2 805 | 2 981 | 720 | 92 | 0 | 8 | |
| 21 M | 10m | Sep. | 0 | 66 | 30 | 103 | 27 | 20 | 92 | 515 | 480 | 4 705 | 520 | 1 145 | 281 | 80 | 169 | 0 | 21 | |
| 22 M | 10m | Sep. | 0 | 553 | 100 | 53 | 26 | 0 | 130 | 220 | 260 | 3 610 | 365 | 795 | 120 | 0 | 320 | 0 | 4 | 1 *Moniezia expansa* |
| 23 M | 22m | Sep. | 6 | 1 588 | 40 | 3 396 | 11 | 20 | 150 | 8 058 | 0 | 7 040 | 0 | 18 285 | 180 | 780 | 61 | 0 | 5 | |
| 24 M | 23m | Oct. | 0 | 462 | 270 | 262 | 12 | 1 | 0 | 540 | 0 | 3 910 | 1 195 | 1 290 | 520 | 855 | 33 | 0 | 1 | 1 *Moniezia expansa* |
| 25 M | 23m | Oct. | 17 | 870 | 450 | 86 | 1 | 0 | 0 | 540 | 0 | 280 | 665 | 120 | 90 | 80 | 2 | 0 | 13 | |
| 26 M | Adult | Oct. | 41 | 320 | 220 | 235 | 0 | 0 | 0 | 0 | 0 | 4 590 | 1 705 | 750 | 385 | 185 | 14 | 0 | 18 | |
| 27 M | 12m | Nov. | 0 | 50 | 61 | 95 | 247 | 0 | 70 | 874 | 154 | 1 330 | 9 022 | 604 | 1 652 | 1 596 | 97 | 0 | 51 | 2 *Moniezia expansa* |
| 28 M | 12m | Nov. | 0 | 110 | 80 | 8 | 540 | 0 | 30 | 581 | 400 | 180 | 3 984 | 301 | 1 063 | 784 | 78 | 0 | 24 | |
| 29 M | 12m | Nov. | 0 | 131 | 131 | 36 | 769 | 0 | 160 | 694 | 100 | 632 | 5 050 | 802 | 1 168 | 1 459 | 112 | 0 | 28 | 3 *Moniezia expansa* |
| 30 F | Adult | Dec. | 11 | 27 | 0 | 320 | 419 | 20 | 0 | 3 692 | 110 | 6 152 | 8 146 | 1 322 | 1 559 | 4 560 | 3 | 20 | 71 | |
| 31 M | Adult | Dec. | 11 | 20 | 70 | 24 | 94 | 0 | 0 | 0 | 0 | 7 243 | 20 | 4 902 | 531 | 30 | 0 | 0 | 0 | |
| | | 1976 | | | | | | | | | | | | | | | | | | |
| 32 F | 1½m | Jan. | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 8 | 6 | 0 | 2 | 0 | 0 | 0 | 0 | 3 *Strongyloides* sp. |
| 33 F | 1½m | Jan. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 4 | 0 | 10 | 0 | 0 | 0 | 0 | |
| 34 M | 1½m | Jan. | 0 | 5 | 9 | 0 | 3 | 0 | 0 | 12 | 13 | 0 | 46 | 0 | 29 | 1 | 0 | 0 | 0 | 5 *Strongyloides* sp. |
| 35 M | 15m | Feb. | 285 | 0 | 20 | 30 | 390 | 0 | 10 | 0 | 0 | 1 290 | 260 | 640 | 120 | 420 | 112 | 1 | 3 | |
| 36 M | 15m | Feb. | 16 | 20 | 40 | 0 | 120 | 0 | 0 | 10 | 0 | 1 520 | 208 | 360 | 350 | 60 | 1 | 0 | 0 | |

4th = Fourth stage larvae M = Male F = Female *C. hungi* = *Cooperia hungi* *C. hamiltoni* = *Cooperioides hamiltoni* *C. hepaticae* = *Cooperioides hepaticae*

(d) More than 4 000 adult *Impalaia tuberculata* were recovered from animals culled during February, November and December 1975. Peak numbers of fourth stage larvae, generally more than 6 000 worms, were recovered from April to September and in December.

(e) Adult burdens of *Cooperia hungi* and *Cooperioides hamiltoni* followed similar patterns, reaching peaks from February to May and during August, November and December 1975. Adult *Cooperioides hepaticae* appeared to be more abundant from July to November. Peak numbers of fourth stage larvae of these three species were recovered from July to September, but since they could not be identified generically they are grouped.

(f) Fourth stage larvae of *Oesophagostomum columbianum* were recovered from animals slaughtered during April, May, July, August and December while the largest numbers of adult worms were encountered during November and December.

One animal harboured four *Fasciola gigantica* and one *Trichuris* sp., two harboured *Gongylonema pulchrum*, two of the three six-week-old impala were infested with *Strongyloides* sp. and nine animals were infested with *Moniezia expansa*.

Table 18 summarizes the mean monthly total burdens of the major genera and the percentage of fourth stage larvae of these worms, excluding *Trichostrongylus* spp., in animals aged 12 months and more.

More than 90 % of the worms were retarded in the fourth larval stage at different times: *Haemonchus placei* from April to September; *Longistrongylus sabie* from April to May and July to October; *Impalaia tuberculata* during May and from July to September; and the *Cooperia hungi/Cooperioides* spp. group of worms during September only.

The animals one to 12 months of age are ranked according to age and their worm burdens are summarized in Table 19.

Only two of the youngest animals had three and five *Strongyloides* sp. respectively, and they also harboured small burdens of *Haemonchus placei*, *Longistrongylus sabie*, *Trichostrongylus* spp., *Impalaia tuberculata*, *Cooperia hungi* and *Cooperioides hamiltoni*.

TABLE 18 Survey 8. The mean monthly total worm burdens of the major genera and percentage of some of these as fourth stage larvae in impala older than 12 months culled in the Nylsvley Nature Reserve near Boekenhout in the northern Transvaal between February 1975 and February 1976

| Month | No of impala examined | Mean numbers of worms recovered | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | *Haemonchus placei* | | *Longistrongylus sabie* | | *Trichostrongylus* spp. | *Impalaia tuberculata* | | *Cooperia* & *Cooperioides* | |
| | | Total | % 4th | Total | % 4th | Total | Total | % 4th | Total | % 4th |
| 1975 | | | | | | | | | | |
| Feb. | 1 | 352 | 29,0 | 230 | 2,2 | 1 527 | 5 976 | 22,2 | 2 479 | 11,3 |
| Mar. | 3 | 332 | 73,2 | 444 | 70,7 | 557 | 4 547 | 58,9 | 5 447 | 62,5 |
| Apr. | 2 | 750 | 95,3 | 198 | 92,4 | 881 | 8 367 | 79,2 | 3 465 | 52,0 |
| May | 1 | 5 053 | 99,7 | 1 100 | 99,9 | 1 648 | 10 775 | 96,1 | 6 135 | 49,1 |
| Jun. | 2 | 1 384 | 96,4 | 574 | 74,7 | 2 314 | 10 715 | 81,6 | 4 297 | 77,7 |
| Jul. | 4 | 1 170 | 99,1 | 2 707 | 99,9 | 1 780 | 10 699 | 91,3 | 6 953 | 87,9 |
| Aug. | 2 | 739 | 100,0 | 539 | 99,9 | 1 427 | 15 358 | 98,1 | 6 818 | 66,7 |
| Sep. | 1 | 1 628 | 97,5 | 3 407 | 99,7 | 8 228 | 7 040 | 100,0 | 19 306 | 94,7 |
| Oct. | 3 | 864 | 63,7 | 199 | 97,8 | 360 | 4 115 | 71,1 | 1 441 | 50,0 |
| Nov. | 3 | 188 | 51,7 | 565 | 8,2 | 1 021 | 6 733 | 10,6 | 3 239 | 17,6 |
| Dec. | 2 | 59 | 40,2 | 429 | 40,1 | 1 911 | 10 781 | 62,1 | 6 454 | 48,2 |
| 1976 | | | | | | | | | | |
| Jan. | – | – | – | – | – | – | – | – | – | – |
| Feb. | 2 | 40 | 25,0 | 270 | 5,6 | 10 | 1 639 | 85,7 | 1 032 | 48,5 |

TABLE 19 Survey 8. The worm burdens of impala up to one year of age culled in the Nylsvley Nature Reserve near Boekenhout in the northern Transvaal between February 1975 and January 1976

| No. and Sex | | Age in months | Month culled | Total numbers of helminths recovered | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | *Haemonchus placei* | *Longistrongylus sabie* | *Trichostrongylus* spp. 4th | *Trichostrongylus axei* * | *Trichostrongylus colubriformis* * | *Trichostrongylus falculatus* * | *Impalaia tuberculata* | *Cooperia* & *Cooperioides* spp. 4th | *Cooperia hungi* * | *Cooperioides hamiltoni* * | *Cooperioides hepaticae* * | *Oesophagostomum columbianum* | Other helminths | |
| 32 | F | 1½ | Jan. 76 | 0 | 1 | 0 | 0 | 2 | 0 | 6 | 0 | 2 | 0 | 0 | 0 | 3 | *Strongyloides* sp. |
| 33 | F | 1½ | Jan. 76 | 0 | 0 | 0 | 0 | 1 | 0 | 4 | 0 | 10 | 0 | 0 | 0 | 0 | |
| 34 | M | 1½ | Jan. 76 | 14 | 3 | 0 | 0 | 12 | 13 | 46 | 0 | 29 | 1 | 0 | 0 | 5 | *Strongyloides* sp. |
| 1 | M | 3 | Feb. 75 | 46 | 0 | 10 | 0 | 50 | 0 | 269 | 60 | 256 | 30 | 0 | 0 | 0 | |
| 6 | M | 5 | Apr. 75 | 645 | 11 | 0 | 25 | 90 | 20 | 2 067 | 547 | 219 | 35 | 9 | 0 | 0 | |
| 7 | M | 5 | Apr. 75 | 282 | 114 | 30 | 16 | 191 | 80 | 2 691 | 358 | 212 | 80 | 33 | 0 | 0 | |
| 10 | F | 6 | May 75 | 496 | 183 | 30 | 275 | 414 | 80 | 2 509 | 612 | 354 | 268 | 33 | 0 | 0 | |
| 12 | F | 7 | Jun. 75 | 472 | 86 | 26 | 130 | 183 | 261 | 3 181 | 907 | 116 | 73 | 4 | 0 | 2 | *Moniezia expansa* |
| 21 | M | 10 | Sep. 75 | 96 | 130 | 20 | 92 | 515 | 480 | 5 225 | 1 145 | 281 | 80 | 169 | 21 | 0 | |
| 22 | M | 10 | Sep. 75 | 653 | 79 | 0 | 130 | 220 | 260 | 3 975 | 795 | 120 | 0 | 320 | 4 | 1 | *Moniezia expansa* |
| 27 | M | 12 | Nov. 75 | 111 | 342 | 0 | 70 | 874 | 154 | 10 352 | 604 | 1 652 | 1 596 | 97 | 51 | 2 | *Moniezia expansa* |
| 28 | M | 12 | Nov. 75 | 190 | 548 | 0 | 30 | 581 | 400 | 4 164 | 301 | 1 063 | 784 | 78 | 24 | 0 | |
| 29 | M | 12 | Nov. 75 | 262 | 805 | 0 | 160 | 694 | 100 | 5 682 | 802 | 1 168 | 1 459 | 112 | 28 | 3 | *Moniezia expansa* |

* Adult worms only M = Male F = Female 4th = 4th stage

As the animals became older they harboured greater burdens of all these helminths except *Strongyloides* sp.

The first *Cooperioides hepaticae* infestations were encountered in five-month-old animals; *Moniezia expansa* was first found in an animal of seven months of age, and *Oesophagostomum columbianum* in impala ten months of age.

Faecal worm egg counts of all impala over six months of age and mean monthly atmospheric temperatures and rainfall are summarized in Table 20.

Egg counts were at a high level from February to April 1975, but a subsequent decrease was followed by a marked rise in November and December.

The highest mean maximum temperatures were recorded from September 1975 to February 1976, and the lowest mean minima during June and July 1975. Rainfall was virtually confined to the warmer months.

## Discussion

This survey yielded four new parasite records for impala, namely *Fasciola gigantica*, *Gongylonema pulchrum*, *Haemonchus placei* and *Trichostrongylus falculatus*. These helminths and *Paramphistomum* sp., *Moniezia expansa*, *Trichostrongylus axei*, *T colubriformis* and *Oesophagostomum columbianum* are usually encountered in sheep or cattle in South Africa. Of the other helminths recovered from the impala, *Impalaia tuberculata* and *Longistrongylus sabie* were found in small numbers in cattle in Survey 7, grazing in the same area as the buck at Nylsvley. From this it is obvious that a considerable overlapping of helminthic fauna parasitic in sheep, cattle and impala occurs. This is not surprising considering the long history of close association between these hosts on farms in South Africa. The large number of helminth species recovered from impala in the present survey, however, is in sharp contrast with the six species only recovered from blesbok in Survey 10 (see below).

Although impala in the present survey and cattle in Survey 7 grazed the same area, albeit in different years, and both acquired *Haemonchus*

TABLE 20 Survey 8. Mean monthly faecal worm egg counts of impala older than six months, atmospheric temperature and rainfall in the Nylsvley Nature Reserve near Boekenhout in the northern Transvaal from February 1975 to February 1976

| Month | Faecal worm egg count e.p.g. | Atmospheric temperature °C | | | Rainfall | |
|---|---|---|---|---|---|---|
| | | Min | Max | Mean | mm | No. of days |
| 1975 | | | | | | |
| Feb. | 6 800 | - | - | - | - | - |
| Mar. | 2 567 | - | - | - | - | - |
| Apr. | 1 450 | - | - | - | - | - |
| May | 200 | 8,3 | 24,1 | 16,2 | 5,7 | 5 |
| Jun. | 700 | 5,1 | 20,6 | 12,9 | 10,6 | 3 |
| Jul. | 50 | 3,1 | 21,0 | 12,1 | 0,0 | 0 |
| Aug. | 300 | 7,0 | 23,7 | 15,4 | 4,5 | 1 |
| Sep. | 433 | 10,9 | 27,8 | 19,4 | 0,2 | 1 |
| Oct. | 433 | 13,4 | 28,9 | 21,2 | 22,3 | 5 |
| Nov. | 3 667 | 15,5 | 29,4 | 22,5 | 57,7 | 13 |
| Dec. | 2 300 | 16,0 | 27,6 | 21,8 | 203,4 | 18 |
| 1976 | | | | | | |
| Jan. | - | 16,5 | 27,9 | 22,2 | 102,6 | 11 |
| Feb. | 100 | 16,3 | 27,8 | 22,1 | 149,7 | 10 |

No climatic data are available for February to April 1975 *placei*, the seasonal incidence of this infestation in the two host species differed considerably in the period from December to February. During this period the highest burdens of *H. placei* were recorded in cattle and the lowest in impala (Compare Tables 16 and 18).

A possible explanation for this difference is that during these months fairly large numbers of adult *Longistrongylus sabie* were present in the impala, thus creating an abomasal environment unsuitable for survival of newly acquired *Haemonchus placei* larvae. Only modest numbers of *Longistrongylus sabie* became established in the cattle and few developed to adults, thus competition between the species did not occur. Competition between *Trichostrongylus axei* and *Haemonchus contortus* to the detriment of the latter species has been described in sheep by Turner, Kates & Wilson (1962) and Reinecke (1974) and a similar phenomenon involving *Longistrongylus sabie* and *Haemonchus placei* may be responsible for the low worm burdens of the latter species in impala.

Marked seasonal arrest in the development of a number of nematode species parasitizing impala was evident in the present survey during the cooler months. Baker & Anderson (1975) recorded this phenomenon in *Ostertagia* spp. infesting white-tailed deer in Ontario, Canada and it was present in *Haemonchus contortus* in blesbok in Survey 10. It is probable that it will be found to occur in many nematode species parasitizing wildlife.

The period of arrested development of *Longistrongylus sabie* was more protracted than that of *Ostertagia* spp. in sheep on irrigated or dry-land pasture (Surveys 3, 4 and 5). The greater percentage of *Longistrongylus sabie* that developed to the adult stage during June indicated a temporary break in inhibition, this was also noted in *Ostertagia* spp. in Surveys 3, 4 and 5.

*Impalaia tuberculata* also exhibited a high degree of arrested larval development during the cooler months.

Unfortunately the fourth stage larvae of *Cooperia hungi* and those of the two *Cooperioides* spp. could not be differentiated but it would appear that inhibition, which was not as marked as in *Impalaia tuberculata*, was present in these helminths from June to September.

It must be remembered that in the present survey the impala were continuously exposed to infestation, and immunity resulting from continual challenge probably also played a role in inhibiting larval development. This postulate is supported by the findings in the majority of young impala, i.e. animals that had been exposed to infestation for a comparatively short time, in which there was a greater proportion of adult worms than in adult animals culled at the same time. Nevertheless, the seasonal pattern of arrested larval development in these young animals was similar to that of older antelope.

The spontaneous development of arrested larvae to adulthood accounts for the rapid rise in egg counts during November and December. Because this increase in pasture contamination coincides with the birth of the impala lamb crop which takes place in November and December, young susceptible animals are exposed to infestation at an early age. The worm burdens and faecal egg counts of the three 12-month-old impala culled during November (Table 17), show that lambs born in the previous year play a major role in contaminating the pasture for the succeeding lamb crop.

Armour (1974) showed that infestation with *Ostertagia ostertagi* acquired during autumn in Scotland caused Type II ostertagiasis in cattle in late winter or spring following the resumed development of fourth stage larvae. The resumed development of arrested larvae of *Longistrongylus sabie* in November and December is comparable with that of *Ostertagia ostertagi* in cattle. The only macroscopic lesions caused by *Longistrongylus sabie* were encountered in impala culled during November and December (early summer). As many as 165 clearly circum= scribed, raised nodules approximately 4 mm in diameter were present in the abomasa of these buck. The mucosal covering of the centre of some of these nodules had eroded and adult parasites extruded through these openings. Intact nodules when opened were found to contain adult parasites coiled in the mucosa. These nodules, which were similar in appearance to those described by Anderson, Armour, Jarrett, Jennings, Ritchie & Urquhart (1965) in calves infested with *Ostertagia ostertagi*, were seen at no other time of the year. Relatively large numbers of arrested fourth stage larvae were present in the abomasal digests in the preceding months, and therefore it seems logical to assume that the nodules were due to the resumed development of these larvae in the abomasal mucosa. The normal, presumably rapid, development of larvae to adults which occurred in February and March did not produce any macroscopicopically visible changes in the abomasal mucosa.

Although *Strongyloides* sp. larvae were recovered from the faecal cultures of a number of impala of all ages, it was only in six-week-old impala that small numbers of these nematodes were recovered and specific identification was impossible. The presence of this parasite in very young buck suggests that the infestation may be milk= borne as is the case with *S. papillosus* in sheep, cattle and goats (Lyons, Drudge & Tolliver, 1970; Moncol & Grice, 1974).

The majority of fourth stage larvae of *Oesophagostomum columbianum* were recovered from antelope culled from April to August and the majority of older impala were infested with adult worms of this species from April to December with peak burdens being recorded in November and December. This seasonal incidence corresponds to that of *O. columbianum* in sheep in South Africa as discussed by Reinecke (1964). No nodules characteristic of *O. columbianum* infestation in sheep were encountered in the small or large intestines of any of the antelope infested with this nematode. The lack of reaction in the gut wall of the impala presents strong evidence that a good host-parasite relationship exists between *O. columbianum* and impala which is not evident in sheep, in which third and fourth stage larvae of *O. columbianum* usually cause nodule formation in the gut wall.

*Moniezia expansa* infestation was confined to those animals slaughtered from April to July and September to November. In sheep exposed to in= festation for limited periods of time major infestations were acquired from February to May and during November (Surveys 3, 4 and 5).

The *Paramphistomum* sp. and *Fasciola gigantica* infestations were most probably acquired from a large marshy area, to which the impala had free access, outside the study site. *Fasciola gigantica* has apparently not been found in wildlife in South Africa (Neitz, 1965), but it has been encountered in wild animals in other countries on the continent (Hammond, 1972).

In her study of the helminths of impala in the Umfolozi area of Zululand Heinichen (1973) noted that a large proportion of the antelope examined were infested with the lung worm *Pneumostrongylus calcaratus*. Although the lungs of all impala in the present survey were examined and processed for the recovery of lung worms, none were encountered.

A comparison of the worm burdens of young impala culled at successive occasions until they reached one year of age made possible the determination of the seasonal availability of infective larvae on the pasture and the variations in worm burdens as the animals acquired new infestations throughout the year. The very young impala shot during January and February would not as yet have been making full use of vegetation as their major source of nutrition, but despite this it can be seen from their worm burdens that larvae of *Haemonchus placei*, *Longistrongylus sabie*, *Trichostrongylus* spp., *Impalaia tuberculata*, *Cooperia hungi* and *Cooperioides hamiltoni* were available during these months. This was confirmed by the worm burdens of five-month-old impala shot during April which had all the parasites listed above and had in the interim also acquired *Cooperioides hepaticae*.

The static nematode burdens of the young impala examined during May or June indicate either that no further infestation with any nematode species was available during these months, or that a balance had been reached between acquisition and loss of infestation. Two *Moniezia expansa*, however, were recovered from the buck culled during June. In September the presence of the larvae of *Trichostrongylus* spp., *Impalaia tuberculata* and *Cooperioides hepaticae* on the pastures was evidenced in the increased worm burdens. Both antelope culled harboured *Oesophagostomum columbianum* and one harboured a single *Moniezia expansa*. In November, in addition to increased numbers of *Trichostrongylus* spp. and *Impalaia tuberculata*, larvae of *Longistrongylus sabie*, *Cooperia hungi* and *Cooperioides hamiltoni* were present on the pastures.

These findings indicate that the colder drier months of May and June and quite probably July and August at Nylsvley are unsuitable either for larval survival or the development of eggs to the infective larval stage on the pastures. The faecal worm egg counts of the impala were generally low during these months, which caused a further reduction in pasture contamination. These results confirm the inability of the free-living stages to develop or survive on pasture at this time and stress the necessity for most species to overwinter as arrested larvae in the host animal in order to survive.

Judging by the condition of the carcasses of the culled impala and the presence of abdominal fat deposits, it did not appear as if their worm burdens had any adverse effect on them. Similar burdens of adult worms in sheep would probably not cause more than a few kg loss in live mass (Horak *et al.*, 1976).

*Survey 9.* *Impala near Pafuri*

## Materials and Methods

*Impala*

Twelve impala of mixed ages and sexes were shot during August 1977.

*Study area*

Pafuri is situated in the north-eastern region of the Kruger National Park and the Transvaal. This is a frost-free region in which impala, kudu and nyala are numerous.

*Helminth collection*

After culling, the carcasses were immediately eviscerated and the rumens examined for paramphistomes. The viscera were transported to a work area where the livers and lungs were processed for helminth recovery. The gastro-intestinal contents were collected, formalin was added and they were stored to be sieved at a later occasion. The gastro-intestinal mucosae were not digested.

## Results

The worm burdens of these impala are summarized in Table 21.

The impala were infested with 13 helminth species, *Bunostomum trigonocephalum*, *Cooperia connochaeti*, *C. hungi*, *Cooperioides hamiltoni*, *C. hepaticae*, *Haemonchus* sp., *Impalaia tuberculata*, *Longistrongylus sabie*, *Oesophagostomum columbianum*, *Strongyloides papillosus*, *Trichostrongylus colubriformis*, *Moniezia benedeni* and *Stilesia hepatica* being recovered.

Many worms were in the fourth stage of larval development and the proportion of fourth stage larvae to adult worms was considerably higher

TABLE 21 Survey 9. The total worm burdens of 12 impala shot near Pafuri in the north-eastern Transvaal during August 1977

| Age | Sex | Number of helminths recovered | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *Haemonchus* sp. | *Longistrongylus sabie* | | *Trichostrongylus colubriformis* | | *Cooperia* /*Cooperiodes* spp. | | | | | *Impalaia tuberculata* | | *Bunostomum trigonocephalum* | *Strongyloides papillosus* | *Oesophagostomum columbianum* | | *Moniezia benedeni* | *Stilesia hepatica* |
| | | | | | | | | *Cooperia hungi* | *Cooperia connochaeti* | *Cooperioides hamiltoni* | *Cooperioides hepaticae* | | | | | | | | |
| | | 4th | 4th | Adult | 4th | Adult | 4th | Adult | Adult | Adult | Adult | 4th | Adult | Adult | Adult | 4th | Adult | Scolices | Scolices |
| 8 mon | F | 25 | 50 | 100 | 0 | 325 | 1 075 | 675 | 150 | 275 | 5 | 800 | 275 | 2 | 150 | 0 | 11 | 0 | 0 |
| 8 mon | M | 0 | 100 | 0 | 0 | 975 | 1 475 | 1 500 | 350 | 775 | 79 | 2 525 | 850 | 1 | 1 375 | 0 | 8 | 0 | 0 |
| 8 mon | M | 25 | 25 | 0 | 0 | 325 | 400 | 250 | 500 | 425 | 63 | 1 075 | 400 | 1 | 1 225 | 0 | 39 | 0 | 0 |
| 8 mon | M | 0 | 50 | 125 | 0 | 100 | 300 | 350 | 225 | 75 | 60 | 200 | 100 | 0 | 0 | 0 | 15 | 2 | 1 |
| 8 mon | M | 25 | 125 | 75 | 25 | 425 | 275 | 450 | 325 | 300 | 32 | 1 775 | 275 | 0 | 325 | 0 | 26 | 1 | 0 |
| 20 mon | M | 0 | 100 | 25 | 0 | 1 450 | 1 275 | 1 075 | 275 | 800 | 46 | 2 275 | 350 | 0 | 825 | 0 | 8 | 3 | 0 |
| Adult | F | 0 | 125 | 0 | 0 | 0 | 2 225 | 100 | 0 | 275 | 0 | 5 500 | 0 | 0 | 200 | 150 | 1 | 0 | 6 |
| Adult | F | 0 | 550 | 75 | 0 | 0 | 2 175 | 75 | 0 | 125 | 6 | 3 925 | 0 | 0 | 0 | 25 | 0 | 0 | 0 |
| Adult | M | 0 | 425 | 0 | 0 | 1 725 | 1 825 | 800 | 775 | 1 900 | 53 | 5 450 | 0 | 0 | 675 | 0 | 64 | 0 | 0 |
| Adult | M | 25 | 125 | 25 | 0 | 300 | 2 150 | 125 | 200 | 950 | 10 | 4 150 | 500 | 0 | 1 150 | 50 | 1 | 0 | 0 |
| Adult | M | 50 | 175 | 25 | 0 | 0 | 1 175 | 100 | 0 | 25 | 0 | 3 325 | 0 | 0 | 250 | 25 | 0 | 0 | 1 |
| Adult | M | 0 | 100 | 0 | 0 | 50 | 1 700 | 125 | 0 | 50 | 0 | 2 700 | 125 | 0 | 375 | 0 | 0 | 0 | 0 |

M = Male

F = Female

4th = Fourth stage larvae

mon = months

in adult impala than in those eight months of age. While all the young impala were infested with adult *Trichostrongylus colubriformis*, *Cooperia connochaeti*, *Cooperioides hepaticae*, *Impalaia tuberculata* and *Oesophagostomum columbianum* many of the adult animals harboured no adult worms of these species.

Three of the five eight-month-old impala were infested with *Bunostomum trigonocephalum*, and three of the six impala 20 months old and younger with *Moniezia benedeni*, whereas none of the adult buck were infested with either of these helminths.

## Discussion

Although only a few animals were examined, and these were all killed during the same month, interesting differences between the worm burdens of adult and young impala are apparent. The large proportion of fourth stage larvae present is due to seasonal arrest in their development during the winter months. The even greater proportion of these larvae recovered from adult animals is due probably to the additional effect of host resistance because of the greater age of the buck and their previous exposure to infestation. Immunity possibly also accounts for the complete absence of adult worms of certain species in some of the adult impala.

The recovery of *Bunostomum trigonocephalum* from young and not from old animals agrees with the findings of Muller (1968) who recovered slightly greater mean burdens of this worm from lambs than from yearlings and adult sheep grazing the same pastures. It is possible that the same factors play a role in limiting infestation with *B. trigonocephalum* in impala as is the case with the hookworm *Gaigeria pachyscelis* in sheep, where previous infestation prevents the establishment of subse= quent infestations even after removal of the initial worm burden (Horak, 1971). The recovery of *Bunostomum trigonocephalum* from impala also constitutes a new host record.

The recovery of *Cooperia connochaeti* confirms the observation of Boomker *et al.* (1979) that this parasite occurs in impala.

*Survey 10.* *Blesbok at Lunsklip*

## Materials and Methods

Blesbok are not indigenous to the Lunsklip area, and in order to leave only indigenous species in the Percy Fyfe Reserve the Department of Nature Conservation, Transvaal Provincial Administration decided to transfer blesbok, which had originally been introduced in this area in 1933, to other reserves. Approximately 750 buck were moved during August and September 1972 leaving 34 animals for survey purposes.

The blesbok in the Percy Fyfe Provincial Nature Reserve grazed a 1 631 ha camp until April 1973; this camp was then joined to another camp, 430 ha in size, containing a herd of roan antelope.

Thirty-two of these blesbok were shot in pairs at intervals of four to five weeks from July 1972 to November 1973. During August and September 1973, however, the interval between culling was only ten days. An attempt was made to cull only male antelope, but this was not always possible. The lungs, livers and gastro-intestinal tracts were transported to the laboratory at Hennops River and processed for worm recovery.

## Results

The buck were numbered from 1 to 32 for convenience and the total worm burdens of each animal are presented in Table 22.

Five nematode and one cestode species were recovered; of these *Impalaia nudicollis* was the most numerous.

*Haemonchus contortus:* Peak burdens of fourth stage larvae were recovered from individual animals during October 1972 and February, March and July to October 1973. Adult burdens exceeded 150 worms in individual animals from August 1972 to March 1973 and again in November 1973.

*Trichostrongylus* spp.: *T. axei* was recovered in small numbers from individual animals virtually throughout the survey period. Peak burdens

TABLE 22 Survey 10. The worm burdens of 32 blesbok culled in the Percy Fyfe Nature Reserve at Lunsklip in the northern Transvaal from July 1972 to November 1973

| Blesbok No. and age | Date culled | Numbers of helminths recovered | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | *Haemonchus contortus* | | *Trichostrongylus* spp. | | *Impalaia nudicollis* | | *Skrjabinema alata* | | *Avitellina* sp. |
| | | 4th | Adult | *T. axei* | *T. falculatus* | 4th | Adult | Imm | Adult | Scolices |
| | 1972 | | | | | | | | | |
| 1 2T | 31 Jul. | 0 | 0 | 0 | 0 | 1 | 622 | 0 | 527 | 6 |
| 2 FM | 31 Jul. | 0 | 0 | 4 | 0 | 7 | 29 | 0 | 61 | 0 |
| 3 FM | 28 Aug. | 6 | 46 | 141 | 9 | 22 | 7 | 0 | 0 | 0 |
| 4 Aged | 28 Aug. | 44 | 501 | 368 | 0 | 1 | 30 | 0 | 0 | 0 |
| 5 2T | 2 Oct. | 40 | 750 | 10 | 460 | 40 | 1 820 | 20 | 261 | 0 |
| 6 4T | 2 Oct. | 420 | 1 320 | 31 | 1 380 | 660 | 3 190 | 170 | 110 | 0 |
| 7 Lamb | 30 Oct. | 0 | 292 | 0 | 594 | 0 | 766 | 1 071 | 0 | 2 |
| 8 4T | 30 Oct. | 245 | 364 | 5 | 0 | 10 | 3 135 | 5 | 0 | 1 |
| 9 Lamb* | 4 Dec. | 30 | 193 | 0 | 542 | 0 | 821 | 381 | 1 124 | 1 |
| 10 Lamb | 4 Dec. | 10 | 253 | 12 | 430 | 11 | 620 | 40 | 340 | 3 |
| | 1973 | | | | | | | | | |
| 11 FM | 8 Jan. | 0 | 175 | 0 | 20 | 0 | 10 298 | 0 | 0 | 0 |
| 12 FM | 8 Jan. | 0 | 206 | 2 | 0 | 5 | 4 330 | 0 | 0 | 0 |
| 13 6T | 5 Feb. | 320 | 760 | 0 | 0 | 95 | 7 840 | 80 | 697 | 0 |
| 14 FM | 5 Feb. | 0 | 590 | 45 | 5 | 20 | 12 880 | 0 | 237 | 7 |
| 15 FM | 5 Mar. | 20 | 80 | 10 | 0 | 10 | 6 413 | 0 | 0 | 0 |
| 16 FM | 5 Mar. | 320 | 195 | 60 | 0 | 228 | 7 220 | 0 | 0 | 0 |
| 17 FM* | 9 Apr. | 0 | 40 | 5 | 0 | 6 | 15 991 | 120 | 106 | 0 |
| 18 6T | 9 Apr. | 0 | 10 | 5 | 0 | 0 | 3 887 | 165 | 105 | 1 |
| 19 2T | 14 May | 25 | 30 | 25 | 15 | 107 | 1 543 | 3 095 | 245 | 1 |
| 20 FM | 14 May | 0 | 25 | 1 | 0 | 45 | 6 898 | 60 | 30 | 0 |
| 21 6T | 18 Jun. | 6 | 1 | 6 | 0 | 23 | 3 120 | 61 | 87 | 0 |
| 22 FM | 18 Jun. | 0 | 0 | 25 | 0 | 20 | 5 068 | 2 | 32 | 0 |
| 23 2T | 25 Jul. | 245 | 2 | 22 | 0 | 103 | 1 021 | 1 | 20 | 0 |
| 24 FM | 25 Jul. | 12 | 2 | 8 | 0 | 10 | 7 773 | 1 | 0 | 0 |
| 25 2T | 27 Aug. | 51 | 0 | 0 | 0 | 39 | 1 812 | 0 | 0 | 0 |
| 26 4T | 27 Aug. | 75 | 0 | 20 | 0 | 53 | 881 | 0 | 0 | 1 |
| 27 4T | 6 Sep. | 250 | 1 | 0 | 0 | 22 | 16 250 | 0 | 0 | 0 |
| 28 4T | 6 Sep. | 833 | 35 | 10 | 0 | 320 | 8 260 | 0 | 0 | 0 |
| 29 2T | 5 Oct. | 11 | 22 | 0 | 0 | 10 | 243 | 0 | 60 | 1 |
| 30 4T* | 5 Oct. | 190 | 123 | 39 | 10 | 60 | 60 | 0 | 0 | 1 |
| 31 Lamb* | 2 Nov. | 20 | 84 | 0 | 400 | 0 | 30 | 2 | 61 | 0 |
| 32 4T | 2 Nov. | 33 | 371 | 0 | 0 | 0 | 930 | 2 | 0 | 0 |

4th = Fourth stage larvae
Imm = Immature worms
* = Ewe
T = Tooth
FM = Full mouth
Lamb = Born during October or November of previous year

of *T. falculatus* were recovered from individual animals from October to December 1972 and during November 1973.

*Impalaia nudicollis:* No seasonal pattern could be determined for the fourth stage larvae of this species. Peak adult burdens usually exceeding 4 000 worms were recorded from January to July and during September 1973.

*Skrjabinema alata:* Occurred in numbers exceeding 200 worms in some animals, while others were not infested. The four blesbok lambs examined were all infested with this nematode.

*Avitellina* sp.: Eleven buck harboured these cestodes and burdens varied from one to seven worms each.

## Discussion

As only six blesbok had originally been introduced in 1933, the helminths that had come with them would have had to be well adapted to blesbok and able to adapt to the local environment in order to survive. This is confirmed by the fact that only six helminth species were recovered in the present survey. Since other animals in the reserve, notably tsessebe and roan antelope, were not examined for helminths, it is not possible to say whether cross-infestation had taken place or whether the latter animals harboured the same species as the blesbok, and could thus serve as an alternative source of infestation.

The seasonal fluctuations in worm burdens in this survey must be conside= red in the light of two factors: firstly, that only two animals were slaughtered on each occasion and, secondly, that the number of blesbok was reduced from approximately 780 to 34 during the first three months of the survey. As a result of this the grazing density altered from approximately one animal/2 ha at the outset to one animal/50 ha during the remainder of the survey. Despite the small numbers of animals examined and the alteration in grazing intensity reducing the chances of infestation, certain trends in the worm burdens emerge.

The presence of peak burdens of adult *Haemonchus contortus* in animals slaughtered from October to March corresponds to observations made on this parasite in surveys in sheep in the RSA (Rossiter, 1964; Viljoen, 1964; Reinecke, 1964).

The presence of fairly large burdens of fourth stage larvae of *H. contortus* and the virtual absence of adults during July to September 1973 indicate inhibition in larval development, although this did not occur the previous year.

The major difference between the *H. contortus* burdens encountered in this survey and those recorded in sheep is numerical. Whereas sheep in the Transvaal generally harbour considerable burdens of this nematode during late summer (Surveys 3, 4 and 5), the worm counts in the blesbok are comparatively low. This could, however, be a reflection of different stocking densities in the various surveys.

The recovery of *Trichostrongylus falculatus* generally from only those animals slaughtered from October to December is difficult to explain and would suggest that this parasite is able to survive on the pasture as eggs or pre-infective larvae during the remainder of the year. In the Karoo, Viljoen (1969) recovered the greatest numbers of *T. falculatus* from tracer lambs grazed during the winter months, thus demonstrating that the free-living stages can survive on the pasture during a period of extremely low rainfall. The seasonal incidence of *T. falculatus* in the present survey is in some respects similar to that encountered for it in cattle near Boekenhout during Survey 7, where the greatest numbers were recovered during December.

Although burdens of *Impalaia nudicollis* varied considerably, the trend appeared to be that total worm burdens increased from January to April. These worms and later infestations probably survived until July or September, after which a decline in reinfestation coupled with death or expulsion of the existing worms resulted in low burdens until the following January.

*Skrjabinema alata* was originally described from sheep by Mönnig (1932). Its prevalence in many animals examined in the present survey would suggest that the blesbok also is a suitable host for this nematode. The same would seem to apply to *Avitellina* sp., but most of the worms recovered, although containing gravid segments, did not exceed 100 mm in length, compared with more than 1,0 m in sheep.

*Survey 11.* *Blesbok at Badplaas*

## Materials and Methods

### *Study area*

The Rob Ferreira Nature Reserve is situated at Badplaas in the eastern Transvaal. The reserve is approximately 400 ha in extent and in addition to blesbok also contained black wildebeest, eland, impala, oribi, springbok, tsessebe and zebra, to a total of approximately 450 animals.

### *Helminth collection*

Two blesbok were shot during May, 11 during June and 15 during July 1978. The carcasses were transported to a large shed where they were eviscerated. The rumens and oesophagi were opened immediately and examined for helminths, while the livers of eight blesbok and lungs and abomaso-intestinal tracts of all were cooled in an insulated container containing dry ice, transported to Onderstepoort and processed for worm recovery.

## Results

The worm burdens of the blesbok, which for convenience have been numbered from 33 to 60, are summarized in Table 23.

The blesbok were infested with 17 helminth species, namely, *Dictyocaulus magnus*, *Gongylonema* sp., *Haemonchus bedfordi*, *H. contortus*, *Longistrongylus albifrontis*, *Trichostrongylus thomasi*, *T. axei*, *T. colubriformis*, *T. falculatus*, *Cooperia hungi*, *C. yoshidai*, *Impalaia tuberculata*, *Oesophagostomum columbianum*, *Agriostomum equidentatum*, *Skrjabinema alata*, *Trichuris* sp. and *Moniezia* sp. Every animal was infested with adult *Dictyocaulus magnus*, *Longistrongylus albifrontis* and *Trichostrongylus thomasi* and fourth stage larvae of *Haemonchus* spp. and *Oesophagostomum* sp. With few exceptions they also harboured adult *Cooperia hungi*, *C. yoshidai* and *Impalaia tuberculata*.

Fourth stage larvae of *Haemonchus* spp. and *Oesophagostomum* sp. constituted the major portion of the worm burdens of these two genera, while large numbers of fourth stage larvae of *Longistrongylus* sp., *Cooperia*

TABLE 23 Survey 11. The total worm burdens of 28 blesbok shot at Badplaas in the eastern Transvaal from May to July 1978

| Blesbok No. | Sex | Egg count (e.p.g.) | Nos. of helminths recovered | | | | | | | | | | | | | | | | | | | Other helminths |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *Dictyocaulus magnus* | | *Haemonchus* spp. | | | *Longistrongylus albifrontis* | | *Trichostrongylus* spp. | | | *Cooperia* spp. | | | *Impalaia tuberculata* | | *Oesophagostomum columbianum* | | *Skrjabinema alata* | | |
| | | | 5th | Adult | 4th | *H. bedfordi* | *H. contortus* | 4th | Adult | 4th | *T. axei* | *T. thomasi* | 4th | *C. hungi* | *C. yoshidai* | 4th | Adult | 4th | Adult | Imm | Adult | |
| Culled 17 May 1978 | | | | | | | | | | | | | | | | | | | | | | |
| 33 | M | 500 | 0 | 18 | 2 168 | 25 | 0 | 368 | 901 | 0 | 0 | 178 | 930 | 459 | 1 800 | 1 723 | 4 777 | 27 | 0 | 1 350 | 1 650 | |
| 34 | M | 300 | 11 | 11 | 4 478 | 151 | 0 | 77 | 650 | 0 | 2 | 412 | 1 203 | 1 205 | 3 376 | 2 417 | 9 304 | 7 | 4 | 1 625 | 5 325 | 2 *Gongylonema* sp. |
| Culled 19 June 1978 | | | | | | | | | | | | | | | | | | | | | | |
| 35* | F | 700 | 2 | 12 | 5 197 | 50 | 0 | 589 | 853 | 0 | 0 | 224 | 1 442 | 1 821 | 1 054 | 2 025 | 3 961 | 37 | 0 | 125 | 275 | 328 *T. colubriformis*<br>1510 *T. falculatus* |
| 36 | F | 100 | 3 | 1 | 4 664 | 0 | 0 | 594 | 427 | 0 | 0 | 216 | 567 | 1 620 | 911 | 3 091 | 8 034 | 35 | 0 | 25 | 0 | 1 *T. falculatus* |
| 37 | F | 100 | 7 | 1 | 1 751 | 0 | 0 | 150 | 175 | 0 | 0 | 81 | 650 | 225 | 734 | 1 428 | 151 | 41 | 0 | 125 | 75 | |
| 38 | F | 200 | 14 | 3 | 4 857 | 0 | 0 | 77 | 1 200 | 0 | 2 | 662 | 1 499 | 1 537 | 1 739 | 2 270 | 6 806 | 109 | 1 | 275 | 525 | |
| 39 | M | 200 | 4 | 9 | 2 626 | 50 | 50 | 675 | 685 | 0 | 0 | 60 | 927 | 646 | 1 185 | 1 639 | 3 946 | 4 | 1 | 0 | 0 | 1 *Moniezia* sp. |
| 40 | F | 100 | 7 | 28 | 3 916 | 26 | 25 | 377 | 1 098 | 1 | 1 | 219 | 611 | 400 | 180 | 226 | 25 | 13 | 0 | 75 | 275 | |
| Culled 28 June 1978 | | | | | | | | | | | | | | | | | | | | | | |
| 41 | F | 400 | 4 | 6 | 6 427 | 50 | 0 | 83 | 800 | 0 | 0 | 420 | 775 | 1 600 | 4 002 | 3 251 | 9 778 | 33 | 2 | 0 | 0 | |
| 42 | F | 300 | 3 | 19 | 5 915 | 25 | 0 | 195 | 1 626 | 0 | 0 | 352 | 25 | 0 | 0 | 0 | 0 | 142 | 1 | 0 | 0 | |
| 43 | F | 500 | 2 | 20 | 5 368 | 25 | 0 | 14 | 900 | 0 | 226 | 550 | 1 525 | 4 975 | 8 600 | 5 053 | 14 575 | 57 | 2 | 0 | 0 | |
| 44 | M | 100 | 0 | 0 | 2 052 | 0 | 0 | 309 | 475 | 0 | 125 | 175 | 229 | 75 | 75 | 1 596 | 2 925 | 3 | 0 | 25 | 350 | |
| 45 | M | 300 | 2 | 6 | 1 587 | 0 | 0 | 128 | 500 | 0 | 0 | 181 | 527 | 2 077 | 975 | 1 407 | 3 950 | 60 | 3 | 750 | 3 750 | |
| Culled 19 July 1978 | | | | | | | | | | | | | | | | | | | | | | |
| 46 | M | 150 | 1 | 8 | 2 048 | 0 | 0 | 129 | 525 | 0 | 2 | 217 | 550 | 253 | 1 200 | 776 | 2 876 | 3 | 5 | 125 | 50 | |
| 47 | M | 50 | 0 | 4 | 2 631 | 150 | 50 | 106 | 450 | 0 | 0 | 227 | 1 152 | 1 205 | 2 181 | 3 005 | 8 354 | 4 | 0 | 0 | 1 | |
| 48 | M | 150 | 0 | 8 | 1 518 | 1 | 150 | 56 | 954 | 0 | 0 | 90 | 425 | 575 | 1 650 | 851 | 2 351 | 55 | 6 | 500 | 325 | 1 *Agriostomum equidentatum* |
| 49 | F | 50 | 21 | 0 | 4 276 | 0 | 0 | 552 | 425 | 1 | 0 | 577 | 951 | 626 | 2 826 | 2 006 | 5 150 | 136 | 0 | 225 | 225 | 1 *Trichuris* sp. |
| 50 | M | 100 | 5 | 2 | 887 | 0 | 75 | 80 | 119 | 0 | 0 | 344 | 504 | 1 050 | 1 000 | 1 437 | 3 550 | 55 | 10 | 0 | 0 | |
| 51 | F | 100 | 4 | 23 | 2 921 | 25 | 0 | 462 | 825 | 0 | 75 | 185 | 950 | 851 | 1 825 | 2 656 | 4 676 | 31 | 20 | 0 | 0 | |
| 52 | F | 0 | 18 | 18 | 3 137 | 25 | 25 | 535 | 275 | 0 | 0 | 276 | 651 | 1 005 | 3 055 | 2 050 | 3 277 | 61 | 0 | 0 | 0 | |
| 53 | M | 0 | 0 | 4 | 3 760 | 0 | 25 | 131 | 500 | 0 | 0 | 402 | 1 001 | 1 125 | 1 130 | 1 745 | 5 329 | 37 | 0 | 225 | 375 | |
| 54 | F | 0 | 3 | 8 | 4 922 | 25 | 50 | 644 | 1 125 | 0 | 0 | 603 | 2 135 | 753 | 4 252 | 4 655 | 9 780 | 2 | 0 | 0 | 0 | |
| 55 | M | 0 | 5 | 5 | 1 905 | 0 | 0 | 179 | 350 | 0 | 0 | 235 | 426 | 1 325 | 752 | 1 775 | 4 275 | 29 | 0 | 50 | 375 | |
| 56 | F | 0 | 11 | 36 | 33 391 | 50 | 175 | 5 992 | 1 150 | 0 | 0 | 2 448 | 14 485 | 2 858 | 6 356 | 225 | 26 | 104 | 1 | 0 | 0 | |
| 57 | F | 0 | 17 | 3 | 8 162 | 0 | 0 | 957 | 1 076 | 0 | 0 | 25 | 50 | 0 | 0 | 3 420 | 4 677 | 6 | 0 | 50 | 75 | 1 *Trichuris* sp. |
| 58 | F | 0 | 6 | 14 | 4 924 | 0 | 25 | 531 | 1 175 | 0 | 0 | 659 | 1 103 | 1 925 | 1 028 | 3 472 | 7 011 | 152 | 2 | 225 | 125 | |
| 59 | F | 0 | 3 | 7 | 3 950 | 0 | 0 | 474 | 751 | 0 | 0 | 451 | 1 009 | 1 200 | 2 175 | 1 831 | 5 278 | 10 | 0 | 0 | 0 | |
| 60 | F | 0 | 5 | 5 | 6 245 | 0 | 50 | 885 | 50 | 0 | 100 | 252 | 2 090 | 2 675 | 2 475 | 4 301 | 6 152 | 118 | 0 | 0 | 0 | |

* Approximately 18 months old
e.p.g. = Eggs per gram of faeces
4th = Fourth stage larvae
5th = Fifth stage worms
M = Male
F = Female
Imm = Immature
*T. colubriformis* = *Trichostrongylus colubriformis*
*T. falculatus* = *Trichostrongylus falculatus*

spp. and *Impalaia* sp. were also recovered.

The first two animals shot had considerably more *Skrjabinema alata* than any other buck, but no other marked differences in worm burden were noticeable between the various slaughter dates, particularly if the burden of Blesbok 56, which harboured an exceptionally large number of worms, is excluded.

## Discussion

The blesbok at Badplaas harboured a greater number and considerably greater variety of parasites than those at Lunsklip. Although other buck ran with the blesbok at both localities, the smaller area of the reserve at Badplaas coupled with the high stocking rate probably accounted for the larger worm burdens and greater number of species recovered.

*Gongylonema* sp., *Trichostrongylus thomasi*, *Cooperia hungi*, *Agriostomum equidentatum*, and *Moniezia* sp. are parasites not previously described from blesbok. No specific identification could be made of the *Gongylonema* sp. or *Moniezia* sp. as only two incomplete worms of the former were recovered and a scolex and a few immature segments of the latter.

*Haemonchus bedfordi* has recently been recovered from blesbok for the first time (Horak, 1978d). Originally described from blue wildebeest and African buffalo by Le Roux (1929), it has been recovered from numerous antelope species (Round, 1968) and does not therefore appear to be particularly host-specific.

*Trichostrongylus thomasi* was originally described from impala (Mönnig, 1932, 1933) and has apparently not been encountered in other species. I have recently, however, recovered it in fairly large numbers from springbok, blue wildebeest and warthog and all blesbok in this survey were infested, indicating a considerably wider host range.

Male worms of *Cooperia hungi* were originally described from waterbuck (Mönnig, 1931a) and females from tsessebe (Mönnig, 1932), and numerous other antelope species are also infested with this worm (Round, 1968).

The impala at Boekenhout and at Pafuri also harboured *C. hungi* and it is probable that if *C. hungi* and *Trichostrongylus thomasi* are not specific parasites of blesbok the presence of a herd of 122 impala in the confined space of the reserve at Badplaas, and presumably harbouring these parasites, ensured that the blesbok became infested.

Until recently *Cooperia yoshidai* had been recovered only from reedbuck (Mönnig, 1939) and mountain reedbuck (Baker & Boomker, 1973). It has subsequently been found in blesbok (Evans, 1978) and its presence in virtually every animal in this survey indicates that it is well-adapted to this host.

Although Mönnig (1932) had recovered *Oesophagostomum columbianum* from blesbok, this was from animals artificially infested with larvae of this worm. Its presence in naturally infested blesbok has, however, been recorded by Fourie (1951) and Ortlepp (1961) and its recovery from a large number of African antelope species (Round, 1968), seems to indicate an old association.

The recovery of a single *Agriostomum equidentatum* from one of the 28 blesbok examined indicates that its presence is probably accidental and a reflection of the fact that 93 springbok, the antelope from which it was originally described (Mönnig, 1929), grazed the reserve with the blesbok,

The presence of *Skrjabinema alata* in blesbok at Lunsklip and Badplaas in the present surveys and in the Rietvlei Nature Reserve near Pretoria (Horak, 1978d) infers that it should be considered a parasite of blesbok although originally described from sheep (Mönnig, 1932).

The large proportion of early fourth stage larvae of *Haemonchus* spp., *Longistrongylus* sp., *Cooperia* spp. and *Impalaia* sp. recovered is probably due to the fact that the animals were all culled during the period May to July (winter) and that these nematodes were overwintering as arrested fourth stage larvae.

The fairly substantial numbers of adult *Longistrongylus albifrontis*, *Cooperia* spp. and *Impalaia tuberculata* recovered from the same animals are probably a reflection of the warm, frost-free winters experienced at Badplaas, making survival outside the host possible and thus possibly removing the necessity for complete inhibition of development in the host during this season. Even these conditions were probably not favourable for the development and survival of the free-living stages of *Haemonchus* spp., and inhibition of development was virtually complete. It seems likely that the same phenomenon accounted also for the large proportion of fourth stage larvae of *Oesophagostomum* sp. recovered.

The low faecal worm egg counts of the blesbok when compared with the fairly large adult worm burdens illustrate the disadvantages of worm egg counts for assessing even adult worm burdens. The absence of eggs recorded for Blesbok 52 to 60 may, however, have been due to the sugar solution used for egg counts in these buck being too dilute to obtain efficient flotation of the eggs.

## *The transmission of nematodes from antelope to domestic livestock*

### Introduction

In many regions of South Africa sheep, goats or cattle graze the same pastures as various species of antelope. Some of the helminths recovered from antelope are those encountered in sheep and cattle (Surveys 3 to 11), while certain helminths of sheep, cattle and antelope seem to be more host-specific and are rarely encountered in other hosts.

Table 24 is a parasite-host check-list compiled for impala and blesbok from Round's (1968) check-lists and findings of the present surveys. It also lists the domestic ruminant hosts (sheep and cattle) from which some of the helminths have been recovered.

The artificial infestation of sheep with the nematodes of a number of antelope species was successfully achieved by Mönnig (1931a, 1932, 1933). He, however, made no mention of the number of infective larvae dosed to the sheep nor of the number of worms recovered at necropsy, and consequent=ly no estimate can be made of the infectivity of the larvae he dosed to the sheep.

Surveys conducted in white-tailed deer and cattle on an island off the coast of Georgia, United States of America (Prestwood *et al.*, 1975) and in white-tailed deer and sheep on common range in West Virginia (Prestwood *et al.*, 1976) indicate that cross-infestation with certain

TABLE 24 A helminth-host check-list for impala and blesbok, and the domesticated hosts (sheep and cattle) from which these worms have been recovered. Data derived from Round (1968) and the findings in this thesis

| Helminth species | Antelope hosts | | Domestic hosts | |
|---|---|---|---|---|
| *Agriostomum equidentatum* | | Blesbok | | |
| *Bunostomum trigonocephalum* | Impala | | Sheep | |
| *Cooperia connochaeti* | Impala | | | |
| *Cooperia fuelleborni* | Impala | | | |
| *Cooperia hungi* | Impala | Blesbok | | |
| *Cooperia yoshidai* | | Blesbok | | |
| *Cooperioides hamiltoni* | Impala | | | Cattle |
| *Cooperioides hepaticae* | Impala | | | |
| *Dictyocaulus magnus* | | Blesbok | | |
| *Gaigeria pachyscelis* | Impala | Blesbok | Sheep | |
| *Gongylonema pulchrum* | Impala | | Sheep | |
| *Haemonchus bedfordi* | Impala | Blesbok | | |
| *Haemonchus contortus* | | Blesbok | Sheep | |
| *Haemonchus krugeri* | Impala | | | |
| *Haemonchus placei* | Impala | | | Cattle |
| *Impalaia nudicollis* | Impala | Blesbok | | |
| *Impalaia tuberculata* | Impala | Blesbok | | Cattle |
| *Longistrongylus albifrontis* | | Blesbok | | |
| *Longistrongylus sabie* | Impala | | | Cattle |
| *Muellerius capillaris* | Impala | | Sheep | |
| *Oesophagostomum columbianum* | Impala | Blesbok | Sheep | |
| *Pneumostrongylus calcaratus* | Impala | | | |
| *Skrjabinema alata* | | Blesbok | Sheep | |
| *Strongyloides papillosus* | Impala | Blesbok | Sheep | Cattle |
| *Trichostrongylus axei* | Impala | Blesbok | Sheep | Cattle |
| *Trichostrongylus colubriformis* | Impala | Blesbok | Sheep | Cattle |
| *Trichostrongylus falculatus* | Impala | Blesbok | Sheep | Cattle |
| *Trichostrongylus minor* | | Blesbok | | |
| *Trichostrongylus thomasi* | Impala | Blesbok | | |
| *Trichuris antidorchi* | | Blesbok | | |
| *Trichuris globulosa* | Impala | | Sheep | |
| | | | | |
| *Avitellina* sp. | Impala | Blesbok | Sheep | Cattle |
| *Moniezia benedeni* | Impala | | | Cattle |
| *Moniezia expansa* | Impala | | Sheep | Cattle |
| *Stilesia hepatica* | Impala | | Sheep | Cattle |
| *Thysaniezia giardi* | Impala | | Sheep | Cattle |
| | | | | |
| *Calicophoron calicophorum* | Impala | Blesbok | Sheep | Cattle |
| *Cotylophoron fuelleborni* | Impala | | | |
| *Fasciola gigantica* | Impala | | | Cattle |
| *Paramphistomum* sp. | Impala | | Sheep | Cattle |
| *Schistosoma mattheei* | Impala | | Sheep | Cattle |

helminth species between deer and domestic ruminants does take place but only to a limited extent. Cross-infestation is of considerable importance where the parasites of one host species may be pathogenic to another, as is the case with the lungworm *Dictyocaulus magnus* of the springbok, which is pathogenic to the bontebok (Verster, 1973, cited by Heinichen, 1973). It is also important where wild antelope serve as reservoir hosts of the common helminths of domestic livestock, which complicates any control programme.

The present experiments describe the artificial infestation of sheep, goats and calves with infective larvae cultured from the faeces of impala culled in Survey 8, and of sheep with larvae from blesbok culled in Survey 10.

## Materials and Methods

### *Donor animals*

Nine impala and eight blesbok culled in Surveys 8 and 10 near Boekenhout and at Lunsklip respectively were used as donors of infective larvae.

Larvae obtained from two impala culled during September and three culled during October 1975 were pooled and used to infest one set of animals, consisting of a lamb, a kid and a calf. Larvae from three impala culled during November were used for a second set of animals, while larvae dosed to a third set were obtained from a single impala slaughtered during December 1975.

Larvae were collected from pairs of blesbok culled on 28 August, 2 October, 30 October and 4 December 1972. Larvae from each pair were pooled separately and dosed to a lamb, different lambs being used for larvae from each pair of blesbok.

### *Infective larvae*

Infective larvae obtained from faecal cultures made from rectal faeces of donor impala and blesbok, were pooled, identified, counted, concentra= ted on filter-paper and dosed to domestic livestock.

*Recipient animals*

The seven lambs, three goat kids and three calves used in these experiments were either raised worm-free or treated with large doses of an anthelmintic and then maintained under worm-free conditions prior to infestation.

*Infestation and slaughter*

On three separate occasions a lamb, a kid and a calf were each infested once with larvae of impala origin. The first set of three animals was infested on 30 October 1975 with larvae obtained from five impala culled during September and October, the second set on 1 December 1975 with larvae from three impala culled during November, and the third set on 29 December 1975 with larvae from a single impala slaughtered during the same month. At slaughter, 32 to 43 days after infestation, egg counts and larval cultures were made from the faeces of the recipient animals.

On 13 September, 13 October, 14 November and 18 December 1972 four different lambs were infested once on each occasion with larvae obtained from pairs of blesbok culled on 28 August, 2 October, 30 October and 4 December 1972 respectively. These lambs were slaughtered 30 to 52 days after infestation.

*Worm burdens*

The worms of donor animals were recovered, identified and counted at slaughter, as were the helminths of the recipients slaughtered later.

## Results

The mean adult worm burdens of the one to five impala from which larvae were obtained to infest each separate set of three animals, the number of larvae dosed, the number of worms recovered from the recipient lambs, kids and calves and the faecal worm egg counts of these animals are summarized in Table 25.

Ten nematode species capable of direct transmission by means of third stage infective larvae were present in the impala from which faeces were

TABLE 25 The worm burdens of donor impala and three sets of recipient lambs, kids and calves infested with larvae cultured from faeces of these impala

| | Nematode species and faecal worm egg counts | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Haemonchus placei* | *Longi=strongylus sabie* | *Trichostrongylus* spp. | | | *Impalaia tuberculata* | *Cooperia hungi* | *Cooperioides* spp. | | *Oesophagosto=mum columbianum* | *E.p.g.* |
| | | | *T. axei* | *T. colubri=formis* | *T. falculatus* | | | *C. hamiltoni* | *C. hepaticae* | | |
| Mean adult worm burden of five donor impala | 202 | 10 | 48 | 1 931 | 96 | 817 | 291 | 396 | 56 | 12 | 500 |
| No. of larvae dosed | 1 560 | 310 | | 5 620* | | 5 770 | | 1 880* | | 160 | |
| No. of worms re= covered from recipient (Lamb 1 | 230 | 0 | 0 | 13 | 0 | 376 | 280 | 14 | 0 | 0 | 10 500 |
| (Kid 1 | 211 | 0 | 0 | 4 | 0 | 120 | 50 | 1 | 0 | 7 | 200 |
| (Calf 1 | 50 | 0 | 0 | 0 | 0 | 0 | 16 | 0 | 0 | 0 | 150 |
| Mean adult worm burden of three donor impala | 91 | 519 | 87 | 716 | 218 | 6 019 | 1 294 | 1 280 | 96 | 34 | 3 650 |
| No. of larvae dosed | 3 230 | 950 | | 1 330* | | 10 830 | | 2 470* | | 190 | |
| No. of worms re= covered from recipient (Lamb 2 | 20 | 205 | 5 | 132 | 40 | 50** | 530** | 33 | 0 | 103 | - |
| (Kid 2 | 20 | 29** | 0 | 0 | 10 | 336 | 21 | 0 | 0 | 3 | 700 |
| (Calf 2 | 0 | 4 | 0 | 20 | 11 | 20 | 91 | 0 | 0 | 0 | 50 |
| Adult worm burden of single donor impala | < 10 | 419 | 0 | 3 692 | 110 | 8 146 | 1 559 | 4 560 | 3 | 71 | 4 100 |
| No. of larvae dosed | 2 280 | 180 | | 1 400* | | 11 560 | | 1 230* | | 350 | |
| No. of worms re= covered from recipient (Lamb 3 | 0 | 0 | 0 | 131 | 0 | 470** | 231** | 0 | 0 | 29 | 100 |
| (Kid 3 | 4 | 0 | 0 | 60 | 0 | 1 049 | 93 | 1 | 0 | 6 | 4 200 |
| (Calf 3 | 0 | 0 | 0 | 32 | 0 | 602 | 82 | 0 | 0 | 0 | 1 550 |

* Larvae identified generically only  E.p.g. = Eggs per gram of faeces

** Many fourth stage larvae

cultured. Of these it was possible to transmit *Haemonchus placei, Longistrongylus sabie, Trichostrongylus colubriformis, T. falculatus, Impalaia tuberculata* and *Cooperia hungi* to lambs, kids and calves. *Cooperioides hamiltoni* and *Oesophagostomum columbianum* were recovered only from lambs and kids, *Trichostrongylus axei* only from lambs and *Cooperioides hepaticae* could not be transmitted artificially.

Despite fairly substantial numbers of larvae of most species being dosed to recipient animals comparatively few worms were recovered. With the exception of *Haemonchus placei, Oesophagostomum columbianum* and in one instance *Trichostrongylus axei,* cross-transmission did not take place when the mean adult burden of a particular species in donor impala did not exceed 200 worms.

The egg counts of eight of the artificially infested animals varied between 100 and 10 500 eggs per gram of faeces and infective larvae of all the abovementioned genera, with the possible exception of *Cooperioides* spp., of which the infective larvae have not yet been described, were recovered from cultures made from their faeces.

The mean adult worm burdens of the two blesbok from which larvae were obtained for each of the four lambs infested,the estimated number of larvae dosed and the number of worms recovered from the artificially infested lambs are summarized in Table 26.

The four nematodes recovered from the blesbok, namely *Haemonchus contortus, Trichostrongylus axei, T. falculatus* and *Impalaia nudicollis* could all be transmitted to sheep, and in general the number of worms recovered in relation to the number of larvae dosed was excellent. However, whenever the mean adult worm burden of a particular species did not exceed 200 worms in the donor blesbok, cross-transmission of that species did not occur.

## Discussion

Mönnig (1933) was able to transmit *Cooperia hungi* artificially from impala to sheep, but there appear to be no accounts of the transmission of other nematodes of impala to domestic livestock. In the present experiment the total numbers of worms recovered from the artificially

TABLE 26 The mean worm burdens of four sets of donor blesbok and of four lambs infested with larvae cultured from faeces of these blesbok

<table>
<tr><th rowspan="3"></th><th colspan="4">Nematode species</th></tr>
<tr><th rowspan="2">Haemonchus contortus</th><th colspan="2">Trichostrongylus spp.</th><th rowspan="2">Impalaia nudicollis</th></tr>
<tr><th>T. axei</th><th>T. falcu=latus</th></tr>
<tr><td>Mean adult worm burden of two donor blesbok</td><td>274</td><td>255</td><td>5</td><td>19</td></tr>
<tr><td>No. of larvae dosed</td><td>1 050</td><td colspan="2">500*</td><td>0</td></tr>
<tr><td>Worm burden of recipient Lamb A</td><td>461</td><td>147</td><td>0</td><td>0</td></tr>
<tr><td>Mean adult worm burden of two donor blesbok</td><td>1 035</td><td>21</td><td>920</td><td>2 505</td></tr>
<tr><td>No. of larvae dosed</td><td>4 860</td><td colspan="2">270*</td><td>3 870</td></tr>
<tr><td>Worm burden of recipient Lamb B</td><td>6 620</td><td>0</td><td>381</td><td>1 914**</td></tr>
<tr><td>Mean adult worm burden of two donor blesbok</td><td>328</td><td>3</td><td>297</td><td>1 951</td></tr>
<tr><td>No. of larvae dosed</td><td>1 950</td><td colspan="2">120*</td><td>1 830</td></tr>
<tr><td>Worm burden of recipient Lamb C</td><td>1 131</td><td>0</td><td>66</td><td>671**</td></tr>
<tr><td>Mean adult worm burden of two donor blesbok</td><td>223</td><td>6</td><td>486</td><td>721</td></tr>
<tr><td>No. of larvae dosed</td><td>2 700</td><td colspan="2">780*</td><td>2 520</td></tr>
<tr><td>Worm burden of recipient Lamb D</td><td>952</td><td>0</td><td>63</td><td>240**</td></tr>
</table>

* Larvae identified generically only

** Many fourth stage larvae

infested animals were small when compared with the total numbers of larvae administered and it seems that cross-transmission between impala and domestic livestock does not readily take place. Adaptive changes for their survival in impala may be responsible for the poor transmission of *Haemonchus placei*, *Trichostrongylus colubriformis*, *T. falculatus* and *Oesophagostomum columbianum* which are normal parasites of cattle or sheep. Similar observations have been made on *Dictyocaulus viviparus*, a parasite normally encountered in cattle. It could not be artificially transmitted to cattle from naturally infested moose (Gupta & Gibbs, 1971) and apparently only in small numbers from elk or black-tailed deer (Presidente, Worley & Catlin, 1972; Presidente & Knapp, 1973).

*Haemonchus placei*, a parasite normally encountered in cattle in South Africa (Surveys 6 and 7) and not in sheep (Surveys 3, 4 and 5), was recovered in greater numbers from artificially infested lambs than from calves, thus indicating some alteration in the host-dependent viability of this nematode. Judging by the numbers of mature worms recovered, goat kids were better alternative hosts for *Impalaia tuberculata* than lambs or calves.

With the exception of *Haemonchus placei* and *Oesophagostomum columbianum*, cross-transmission generally did not take place when the adult worm burden of a particular species in the donor impala was less than 200 worms. This can be ascribed to the fecundity of the female worms of the various species, and hence their contribution to the larval pool from which the larval doses were made up. Both *Haemonchus* and *Oesophagostomum* species are prolific egg layers (Gordon, 1948), and thus a few adult females would make a considerable contribution to the larval pool. The other species, being less fecund, would contribute fewer larvae. Consequently the chances of cross-transmission would be minimal from those donor animals in which only a few adult worms of the other species listed in Tables 25 and 26 were present.

The presence of fairly high faecal worm egg counts and of infective larvae of most nematode genera of impala origin in the faecal cultures of artificially infested animals shows that these parasites can complete their life cycles in domestic livestock.

The results of Surveys 7 and 8, conducted in cattle and impala utilizing the same pasture, suggest that very little natural cross-transmission occurs. Because *Haemonchus placei* and *Trichostrongylus* spp. occur naturally in both hosts, however, it is not possible to say what role cross-infestation plays in maintaining the parasitic levels of these helminths in either host.

The artificial infestation of lambs with *Haemonchus contortus*, *Trichostrongylus falculatus* and *Impalaia nudicollis* of blesbok origin confirms the results of similar experiments conducted by Mönnig (1932). He stated then that apparently *I. nudicollis* did not readily adapt itself to sheep. The present results indicate that although the number of *I. nudicollis* recovered from lambs was high when compared with the number of larvae dosed, many of these worms did not mature. This would probably account for the absence of *Impalaia* sp. larvae from the faeces of the first sheep that Mönnig (1931a) infested with larvae from blesbok.

The numbers of *Haemonchus contortus*, *Trichostrongylus axei* and *T. falculatus* recovered from blesbok and lambs indicate that these nematodes are well adapted to both species and that cross-transmission can readily take place. The blesbok from which the larvae were cultured had possibly had no contact with sheep for at least 40 years and yet no difficulty was experienced in cross-transmitting these species.

The numbers of *Haemonchus contortus* and *Trichostrongylus falculatus* recovered from Lamb B (Table 26) were larger than the estimated number of infective larvae used for infestation. This was probably due to more infective larvae being dosed than were estimated.

## GENERAL DISCUSSION OF HELMINTHS IN RUMINANTS

### SURVEY METHODS

The methods employed to study the epizootiology of helminth parasites of ruminants have evolved from comparatively simple procedures to fairly sophisticated techniques and have generally been based on determining either the seasonal incidence of parasites in their hosts or the seasonal availability of infective larvae on pasture. More recently combinations of these methods have been utilized with considerable success.

*The incidence of parasites in their hosts*

(i) Faecal worm egg counts

Numerous workers have attempted to establish the seasonal incidence of helminth parasites by the regular collection of faecal samples and the preparation of faecal cultures for differential worm egg counts (Gordon, 1948, 1953; Meldal-Johnsen, 1961; Hobbs, 1961; Rossiter, 1961; Muller, 1964; Thomas, 1968; Swan, 1970). The reliability of this method has been questioned by several authors (Gordon, 1948; Muller, 1961; Reinecke, 1963; Brunsdon, 1970, 1971). Not only do faecal worm egg counts frequently bear little relationship to the number of adult worms present, but the fecundity of the various species must be taken into consideration when assessing the significance of a high or low egg count. An even greater disadvantage is their inability to demonstrate the presence of immature worms.

Without faecal worm egg counts, however, it would be difficult to determine such important phenomena as self-cure of helminth infestation, spring and periparturient rise in egg count or the degree of contamination of the pasture caused by a flock of sheep or herd of cattle.

(ii) Examination of viscera at abattoirs, knackeries or animal health laboratories.

The examination of material from these sources as described by Brunsdon (1964), Ross (1965, 1966), Thomas, Nunns & Boag (1970), McKenna, Campbell, Mason, Rutherford & Picard (1974) and Henderson & Kelly (1978) has certain inherent disadvantages. The animals examined in consecutive weeks or months most probably do not come from the same locality and considerable variations in parasite loads can be expected where marked geographic and climatic differences occur within a region served by the abattoirs or laboratories. In addition the age of the animals and their treatment prior to slaughter or death are unknown. The fact that material from knackeries and laboratories frequently comes from diseased animals must also be taken into account as these animals cannot be considered truly representative of a given region.

Such surveys are, however, valuable in indicating the helminth species that may be encountered in a particular area and where the area served is limited or climatic variations small, certain trends for some species may become obvious (Ross, 1965).

(iii) Regular slaughter of animals from a particular locality

The epizootiology of helminth infestations can be determined by the regular slaughter of animals selected from a single continuously exposed flock or herd within a given locality. This has been done in sheep by Parnell (1962), Barrow (1964), Rossiter (1964), Viljoen (1964) and Ayalew & Gibbs (1973), in cattle by Brunsdon (1972), in white-tailed deer by Baker & Anderson (1975) and in buffalo by Bindernagel & Todd (1972). In some of these surveys regular faecal worm egg counts were done on animals from the flock or herd.

The advantage of this survey method is that the worm burdens reflect the degree and type of infestation that will be encountered in animals exposed naturally in that particular environment. Because infestation has generally been acquired over a long period, short-term fluctuations in climate or alterations in husbandry practices will not have a drastic influence on the worm burdens. The size and composition of the worm burdens are determined by the interactions of host-immunity, availability of infestation, cross-infestation and climate. When this survey method is accompanied by faecal worm egg counts the latter can be related to the relative fecundity of the various species and phenomena such as self-cure and spring or periparturient rise in egg count can be assessed from the composition of the worm burden and the alteration in egg counts.

The disadvantage is that the time of acquisition of each species cannot be determined and thus the influence of recent climatic or husbandry changes on worm burden cannot easily be assessed. If large numbers of fourth stage larvae are present it is not possible to determine whether they were recently acquired, or arrested in their development because of climatic conditions prevalent at the time of their acquisition (Armour & Bruce, 1974), or because of the effects of acquired host-resistance (Donald, Dineen, Turner & Wagland, 1964), or host age (Herlich, 1960; Viljoen, 1969).

This is, however, the most practical method for determining fluctuations in the worm burdens of free-ranging antelope.

*The seasonal fluctuations of infective larvae on pasture*

(i) The recovery of infective larvae from pasture.

The seasonal fluctuations of infective larvae of several nematodes parasitising sheep have been determined on pasture by Gibson (1966) and Gibson & Everett (1967, 1971, 1972, 1976) and of cattle by Michel, Lancaster & Hong (1970a). Although these studies are invaluable for assessing the effect of climate and husbandry on development and survival of larvae on pasture they do not indicate whether or not the infective larvae are viable and cannot project whether or not they will be ingested by grazing animals.

A further limitation of this method lies in the fact that larvae are not randomly distributed on pasture (Crofton, 1954; Donald, 1967) and consequently only quite large differences between the means of two random sample estimates are likely to be significant (Donald, 1967).

(ii) Tracer animals

Tracers may be animals raised and maintained worm-free, or rendered worm-free by the administration of a highly effective anthelmintic and thereafter maintained under worm-free conditions, or kept at pasture but treated at regular short intervals with a highly effective anthelmintic. They are exposed in consecutive groups to natural infestation for a short period of time and then slaughtered.

This survey method has been employed by Tetley (1959), Thomas & Stevens (1960), Michel *et al.* (1970b), Connan (1971), Brunsdon (1972), Reid & Armour (1972) and Smith (1974). It supplies data on the seasonal availability of larvae, the seasonal changes between species and the seasonal course of arrested development in the host.

Because the tracers are exposed for a comparatively short while, resistance brought about by continuous exposure to infestation is unlikely to play a major role in inhibiting larval development or limiting worm burdens. The slaughter of tracer animals without doing pasture larval counts does not permit a comparison of the number of larvae ingested with the number of worms that become established, nor does it reflect what the worm burdens of animals continuously exposed to infestation at the same locality will be.

*The seasonal fluctuations of parasites on pasture and in their hosts*

The survey conducted during 1960 and 1961 by Muller (1968) is probably the first attempt to determine not only the seasonal availability of larvae to tracer lambs but also seasonal fluctuations in worm burdens of continuously exposed lambs grazing the same pastures. He further refined his experiment by including a group of continuously exposed adult sheep, thus permitting a comparison of the worm burdens of lambs and adult sheep.

Viljoen (1969) also slaughtered tracer lambs and continuously exposed lambs utilizing the same pasture. Both Muller (1968) and Viljoen (1969) compensated for the effect of reduced grazing pressure which would have occurred with removal of animals for slaughter by replacing them with other sheep.

Boag & Thomas (1971) and Thomas & Boag (1972) followed the course of infestation on clean and autumn- or spring-contaminated pastures by doing faecal worm egg counts in ewes and lambs, pasture larval counts, determining lamb weight gains and slaughtering lambs for total worm counts at the termination of their experiments. In a similar experiment Donald & Waller (1973) examined the effect of four methods of pasture contamination on pasture larval counts, ewe and lamb faecal egg counts, lamb weight gains and the worm burdens of lambs at weaning.

In a more sophisticated experiment Waller & Thomas (1975) studied the epidemiology of *Haemonchus contortus* in lambs reared with infested ewes under field conditions. Infestation was monitored by pasture larval counts, faecal egg counts in ewes and lambs, and the slaughter of lambs continuously exposed to infestation and of tracer lambs.

The importance of the abovementioned experiments is the contribution they have made to an understanding of the source of infestation available to the lamb emanating from the ewe or resulting from various husbandry practices, and the rapidity with which eggs are translated into available infective larvae.

In probably one of the most elegant experiments conducted to date Southcott *et al.* (1976) contaminated each of seven separate plots of pasture for one month during seven different months of the year. They determined the total differential faecal egg output of the contaminating sheep and the worm burdens of sets of tracer lambs allowed to graze the plots for two weeks during a period of 12 months after contamination of the plots. This experiment made it possible to assess the rate of translation of eggs into available infective larvae, the relationship between total egg contamination and larval acquisition, survival of infestation on pasture and the effect of seasonal climatic changes on development of infestation in tracer lambs. The inclusion of a group of continuously exposed animals slaughtered at regular intervals would significantly have added to the results obtained from the experiment.

### *The present surveys*

The present surveys in sheep and cattle can be criticised in that while tracer animals supplied data on seasonal availability of infective larvae no continuously exposed animals were slaughtered to indicate the seasonal fluctuations of worms within the host. Although differential faecal worm egg counts done on continuously exposed animals in Surveys 3 to 5 and 7 partly compensated for this omission, they could give an indication only of the species of adult worms present and no inkling of the level of larval infestation. The surveys were also not devised to determine survival of infestation on pasture.

In the surveys in impala near Boekenhout and blesbok at Lunsklip seasonal fluctuations of worm burdens in continuously exposed hosts could be determined. The absence of tracer animals, for obvious reasons, preclude estimation of larval availability. Tracer cattle slaughtered during the following year near Boekenhout partially made up for this deficiency in that certain parasites of impala were recovered from these animals.

The results of the surveys in impala and blesbok near Pafuri and at Badplaas respectively stress the value of slaughtering a large number of animals on each occasion if continuously exposed animals are used for survey purposes. By doing this individual variation in worm burden becomes less important. It must, however, be stressed that time usually precludes examination of a large number of individuals. In my laboratory the processing and examination of a single animal takes between one and three man-days depending upon the number of worms and number of species present.

## *THE INCOMPLETE VIEW*

An important but largely unnoticed feature of research into the epizootiology of parasitic infestations is the compartmentalization into the separate disciplines of helminthology, entomology, acarology and protozoology that has occurred. Indeed subdivisions within each of these fields are also recognisable, cestodes, nematodes and trematodes being treated separately, as are biting flies and myiasis-producing flies, ticks and mites, intestinal, blood and skin-dwelling protozoa. Each of these can be divided into even narrower fields with often only a single parasite being studied, or only abomasal parasites, or parasites of the sinus cavities, among many other examples.

Thus James & Johnstone (1967) studied the epizootiology of *Ostertagia circumcincta* in sheep, Michel *et al.* (1970b) arrested development of *Cooperia oncophora* in calves, Worley *et al.* (1974) the acquisition of *Moniezia expansa* by sheep, Rogers & Knapp (1973) the seasonal incidence of larvae of the nasal bot fly, *Oestrus ovis*, in sheep, Connan (1971) that of *Haemonchus contortus* and *Ostertagia* spp. in sheep and Brunsdon (1972) inhibited development of *Ostertagia* spp. and *Cooperia* spp. in calves. Bindernagel & Todd (1972) examined only the abomasa of 165 buffalo in Uganda and Baker & Anderson (1975) those of 43 white-tailed deer in Canada. (The latter animals were, however, also examined for lice: Watson & Anderson, 1975). During surveys on the seasonal incidence of helminths in sheep conducted over periods of two years in three separate localities Viljoen (1969) mentions that *Trichuris* sp. and *Moniezia* spp. were recovered but does not include them in his otherwise thorough counts of worms. Indeed the various survey methods discussed earlier in this thesis are designed to determine the epizootiology of parasitic nematodes and do not take other parasites into account.

The foregoing lists but a few examples of the wastage of valuable material occasioned by parasitological surveys. If one were to add to this the equal or even greater wastage of common, rare and endangered species of wildlife slaughtered merely for collection, often without enumeration, of one or a few parasite species, or measurement of growth or other factors, or determination of the composition of ruminal micro-flora or contents, a picture of wanton destruction rather than scientific endeavour emerges.

In an attempt to obtain as many data as possible from each necropsy some of the animals slaughtered in the present series of surveys were examined also for ectoparasites. Thus sheep in Surveys 4 and 5 were examined for the larvae of *Oestrus ovis* (Horak, 1977) and blesbok in Surveys 10 and 11 for larvae of *Oestrus* spp. and *Gedoelstia hässleri*, nasal bot flies of certain alcephaline antelope (Horak & Butt, 1977). The cattle and impala slaughtered in Surveys 7 and 8 were processed for the recovery of all permanent ectoparasites and these results will be published separately. With the exception of the hippoboscid fly *Lipoptena binoculus* on impala, no collections of biting flies parasiti= zing either host were made because of the special techniques required for their capture, nor were examinations for protozoan parasites carried out. Measurements to determine age and condition were taken from each impala and ruminal contents were collected from the cattle and impala to determine what vegetation they had consumed and composition of their ruminal micro-organisms.

The complete parasitological picture is important not only because of possible interactions which may occur between widely differing parasites {for instance prior infestaion with *Dictyocaulus filaria* may adversely affect the establishment of *Gaigeria pachyscelis* (Horak, 1971)}, but also because the presence of one species may result in conditions which are attractive for another. Thus larvae of the blowflies *Lucilia cuprina* and *Chrysomyia chlorophyga* cause primary cutaneous myiasis in sheep and only then do these sites become attractive to the secondary blowfly *Chrysomyia albiceps* which deposits its eggs on the lesions (Mönnig, 1934).

Wounds caused by the long mouthparts of the ticks *Amblyomma hebraeum* and *Hyalomma* spp. are attractive to the screwworm fly *Chrysomyia bezziana* which then deposits its eggs on them and gives rise to myiasis (Zumpt, 1965). The presence of ticks should also always be considered in the light of protozoal or rickettsial diseases which they may transmit.

Many of the parasitic helminths can cause a drop in productivity (Snijders *et al.*, 1971; Horak *et al.*, 1976; Hawkins & Morris, 1978), as can the larvae of the flies *Oestrus ovis* in sheep (Horak & Snijders, 1974) and *Chrysomyia bezziana* in cattle (Horak, Londt & Stewart, 1976, cited by Huntley, 1977), the sheep ked, *Melophagus ovinus* (Nelson & Slen, 1968), and the tick *Amblyomma maculatum* on cattle (Williams, Hair & McNew, 1978), as well as protozoa belonging to the genus *Eimeria* (Marlow, 1968).

The results of surveys on cattle and impala near Boekenhout, and on wildebeest in the Kruger National Park in which both internal and external parasites were recovered, illustrate the wide variety of parasites that may be recovered. The cattle were infested with 11 helminth species and eight species of ticks; the impala with 16 helminth species, six species of ticks, three lice species and a biting fly; the wildebeest with 16 helminth species, six tick species, three species of lice, a mite, the nymphae of a pentastomid, and the larvae of five species of oestrid flies.

Having personally been responsible for the slaughter of thousands of sheep and hundreds of cattle and wild ruminants, most of which could have been more thoroughly utilized, I feel that a much more extensive approach is necessary, particularly when wild animals are culled for research purposes, in order to obtain the maximum benefit from the available material.

## *HOST SPECIFICITY AND PARASITE DISTRIBUTION ACCORDING TO CLIMATE*

It is not the intention of this discussion to review host specificity in great detail but rather to speculate on its implications for the present surveys.

Cameron (1964) stated that host specificity is one of the fundamental characteristics of parasitism but it is seldom absolute, and to a variable degree it is relative. Moreover when hosts have evolved from a common ancestor, the parasites of that ancestor will evolve with the hosts, so that the modern descendants of that ancestor will tend to have descendants of its parasites. Host specificity also reflects the interplay of ecological factors, host behaviour and intrinsic determinants such as the physiology, nutrition and immunological status of the host (Hudson, 1973).

Because of their common ancestor the various ruminant species are likely to harbour parasites from the same family or even genus. Cross-transmission with these helminths will occur provided the hosts are fairly closely related and intrinsic determinants in the new host permit a viable association to develop. This will also occur between more distantly related species which regularly utilize the same habitat and harbour related species of parasites. It is well-illustrated in sheep and cattle in which certain species can give rise to viable infestations in the alternate host (Surveys 3, 5 and 6).

Many old host-parasite associations have developed because of geographic isolation, while new associations have occurred because of the migration of man and his livestock.

The parasites of domestic livestock in Europe have developed with their hosts and because of the paucity of wild animals in the last centuries, most associations are comparatively old and the parasitic fauna of sheep and of cattle clearly defined. The same is not true of Africa where domestic animals, some of which originate from Europe, often mingle with wild animals and old and new associations may exist in the same animal.

Host-specificity is not easy to determine; it requires the examination of a large number of animals in various localities, the recovery of both adult and immature parasites, their enumeration and identification and possibly also artificial cross-transmission to determine their infectivity for other hosts. Most host-parasite check-lists merely indicate that a particular parasite has been recovered from a particular host, but cannot be considered to indicate host-specificity because their compilation usually does not meet the requirements listed above.

To make these lists more meaningful I suggest that the parasites should be grouped as follows:-

(i) Definitive parasites: These are prevalent in a large percentage of the population, often in fairly large numbers and are capable of reproduction and a long period of survival.

(ii) Occasional parasites: Are present in variable numbers in some of the population. They may be capable of reproduction but their survival period in the host is often limited. When related host species, harbouring related parasites, mingle in the same habitat this type of association is frequently encoun= tered.

(iii) Accidental parasites: These are usually present in only a small percentage of the population and then usually in small numbers. They may not be capable of development to adulthood and if they are, may not reproduce, and their period of survival in the host may be very limited. Accidental parasitism occurs when different hosts mingle in the same habitat and large numbers of infective larvae are available. Neither the hosts nor their parasites need be closely related.

The grazing experiments conducted by Barger & Southcott (1975) and Southcott & Barger (1975) demonstrated the difference between definitive and occasional host-parasite associations. They utilized sheep or cattle to decontaminate the pastures previously grazed by the alternate host and found that the sheep parasites *Haemonchus contortus* and *Trichostrongylus colubriformis* were present in calves grazed for one month on pastures previously contaminated by sheep, but not when they were grazed for two months. They suggested that the longer period of grazing may have permitted development of resistance and consequent eli= mination of infestation. Similarly *Cooperia* spp. in sheep in Surveys 3 and 5 can be considered occasional parasites although no attempt was made to determine their longevity in the sheep.

Climate was probably an important factor in the geographical isolation that led to the evolution of helminth species. Its role today is as important in determining the distribution of these species. Thus generic and even specific climatic requirements may determine the distribution of parasites within a given region. These climatic requirements not only directly influence the distribution of helminths by their effect on the free-living stages but also indirectly in that they influence the habita of the hosts and hence their distribution.

The cattle parasite *Ostertagia ostertagi* is found in the winter rain=

fall regions of the Cape Province and on irrigated pastures on the Transvaal Highveld (Horak, Unpublished data) while *Haemonchus placei* and *Oesophagostomum radiatum* are found in most summer rainfall regions of the RSA (Reinecke, 1960b; Hobbs, 1961; Surveys 6 and 7). The sheep parasite *Trichostrongylus falculatus* thrives in the semi-arid Karoo (Viljoen, 1964, 1969), while *T. colubriformis* and *T. rugatus* are found in large numbers in the moister regions of the Cape Province (Barrow, 1964; Rossiter, 1964). *Oesophagostomum venulosum* is found in sheep in the winter and non-seasonal rainfall regions of the Cape Province (Muller, 1968; Snijders *et al.*, 1971) and *O. columbianum* in the summer rainfall regions of the RSA (Barrow, 1964; Rossiter, 1964; Viljoen, 1964; Surveys 3, 4, 5, 8, 9, 11).

Because of climatic differences, host-parasite check-lists drawn for particular regions within a country will differ from those for other regions. It is therefore important when compiling such a list for a country as a whole that the regional distributions of the parasites be given.

The RSA is divided into 12 climatological regions (Fig. 9). It can also be divided into six biotic zones (Rautenbach, 1978). These biotic zones have been defined by Rautenbach (1978) as "zones and subzones (that) have been empirically derived by considering main vegetation types and how they best fit the distribution of species, initially of birds and later of mammals."

Whereas the conditions within a single or a number of biotic zones will determine the distribution of free-ranging antelope, the same conditions will only affect the density of domestic livestock and not its presence within a zone as man has largely ignored the zonal boundaries in his quest for grazing. In many instances he has also introduced antelope into regions outside their normal biotic zones (Ansell, 1971).

Thus in broad terms it can be stated that the distribution of parasites of domestic livestock will be influenced mainly by climate, while that of helminths of free-ranging antelope will be influenced by climate and the biogeographical distribution of their hosts.

Combining the findings of the present surveys with those conducted by Reinecke (1960b), Hobbs (1961), Barrow (1964), Rossiter (1964), Viljoen

(1964, 1969), Muller (1968), Young & Wagener (1968), Snijders *et al.* (1971), Heinichen (1973, 1974) and with numerous unpublished personal observations, it is possible to compile host-parasite check-lists for sheep, cattle, impala and blesbok in the RSA. In these lists the helminths are classified as definitive, occasional and accidental parasites and their distribution according to climate is given.

The helminths of sheep and their distribution based on the climatic regions given in Fig. 9 are listed in Table 27.

The definitive nature of some associations is confirmed by recovery of the same helminths from sheep in surveys in the United Kingdom where cross-infestation from antelope is unlikely. Thus *Bunostomum trigonocephalum* (Boag & Thomas, 1971), *Chabertia ovina* (Connan, 1974), *Cooperia curticei* (Reid & Armour, 1975), *Dictyocaulus filaria* and *Muellerius capillaris* (Thomas *et al.*, 1970), *Haemonchus contortus* (Connan, 1971), *Nematodirus filicollis* (Reid & Armour, 1972), *Oesophagostomum venulosum, Ostertagia circumcincta, O. trifurcata, Trichostrongylus axei, T. colubriformis, T. vitrinus* (Reid & Armour, 1975) and *Fasciola hepatica* (Ross, 1967) have all been recovered from sheep in the United Kingdom and in South Africa.

*Fasciola gigantica* is listed as an occasional parasite of sheep for although it can complete its life cycle in this host it is highly pathogenic for sheep and many may succumb to even moderate infestations (Horak, Snijders & Louw, 1972). Similarly *Schistosoma mattheei* is pathogenic for sheep and even small risidual worm burdens may eventually lead to death (Van Wyk: Personal communication). Such unstable relationships cannot be considered typical of a definitive association and consequently are classified as occasional. It is perhaps signifi= cant to note that few sheep are found in the regions in South Africa inhabited by these two parasites and that definitive associations may not have had time to develop.

The helminth parasites of cattle are presented in Table 28.

Surveys conducted in cattle in Australia and the United Kingdom con= firm that *Bunostomum phlebotomum, Cooperia pectinata, Haemonchus placei, Oesophagostomum radiatum* (Henderson & Kelly, 1978), *Dictyocaulus viviparus* (Michel, 1955), *Nematodirus helvetianus, Ostertagia ostertagi, Trichostrongylus axei* (Anderson *et al.*, 1965) and

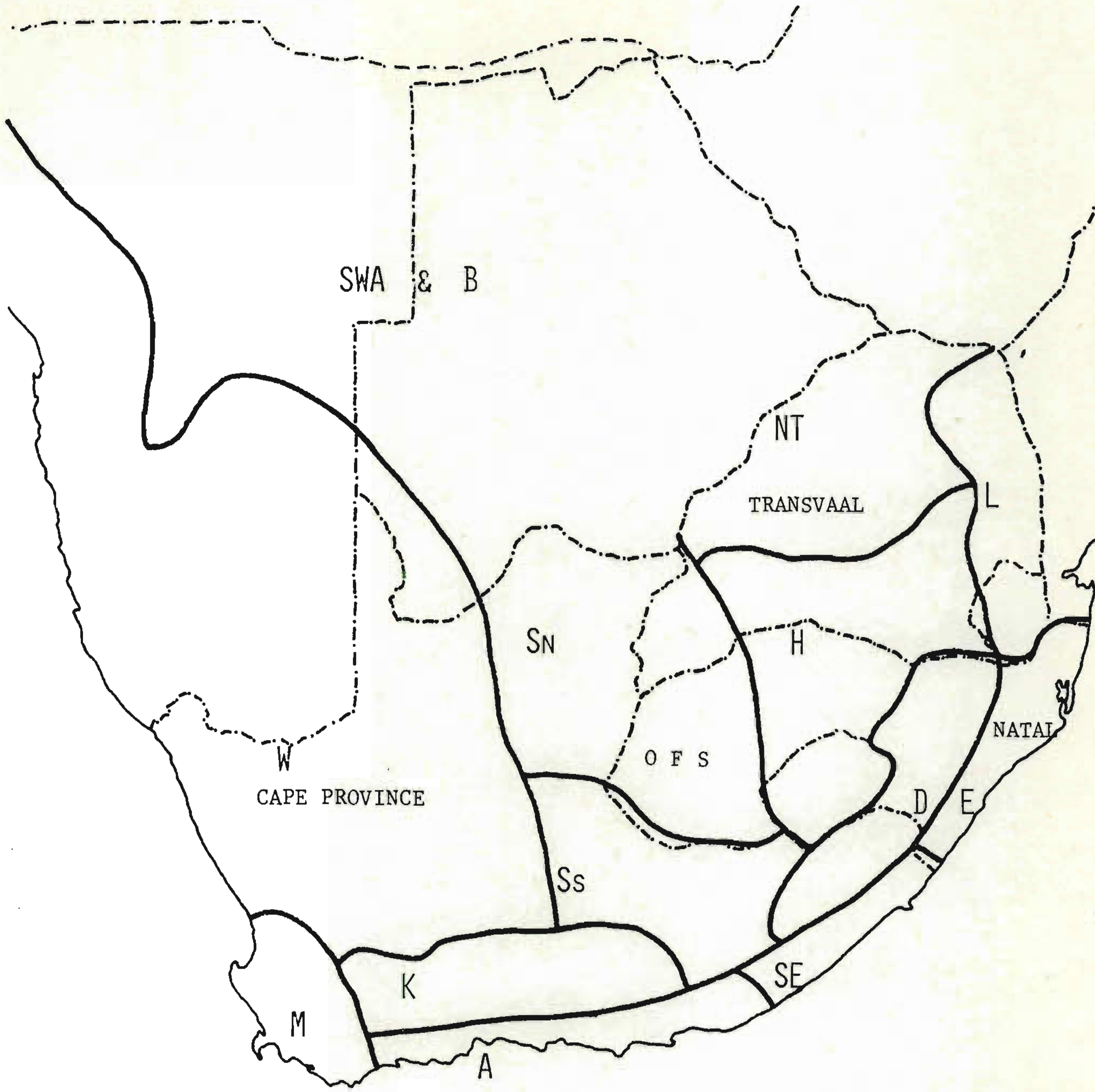



Fig. 9 The climatological regions of the Republic of South Africa (Compiled by the Climatology Branch, Weather Bureau, Pretoria 1956) M = Winter rains, hot dry summer. A = Temperate, warm and moist, occasional hot and dry "bergwinds". K = Desert and transition zone from winter to summer rains. SE = Warm, temperate and moist. E = Warm and moist. D = Warm, temperate monosoonal type of climate. L = Subtropical, warm and muggy except in midwinter. NT = Subtropical, semi-arid. H = Warm, temperate monsoonal type of climate, dry winter. Ss and Sn = Semi-arid, summer rains. SWA and B = Climate similar to that of Ss and Sn. W = Desert

TABLE 27 Definitive and occasional helminth parasites of sheep and their distribution in the RSA according to climate. For distribution code see Fig. 9

| Helminth species | Distribution |
|---|---|
| Definitive | |
| *Bunostomum trigonocephalum* | H,A |
| *Chabertia ovina* | A,M |
| *Cooperia curticei* | A |
| *Dictyocaulus filaria* | H,D,E,SE,A,M |
| *Gaigeria pachyscelis* | Sn,W |
| *Haemonchus contortus* | NT,H,D,E,SE,A,Ss,Sn,W |
| *Marshallagia marshalli* | A,K,Ss |
| *Muellerius capillaris* | A |
| *Nematodirus filicollis* | A |
| *Nematodirus spathiger* | A,K,Ss,W |
| *Oesophagostomum columbianum* | NT,H,D,E,SE,K,Ss,Sn,W |
| *Oesophagostomum venulosum* | A,M |
| *Ostertagia circumcincta* | SE,A,M,K,Ss |
| *Ostertagia trifurcata* | SE,A,K,Ss |
| *Strongyloides papillosus* | H,Sn,W,A |
| *Trichostrongylus axei* | SE,A |
| *Trichostrongylus colubriformis* | H,D,SE,A,M |
| *Trichostrongylus falculatus* | NT,H,Sn,Ss,W,K,A |
| *Trichostrongylus pietersei* | A,SE |
| *Trichostrongylus rugatus* | H,Ss,SE,A |
| *Trichostrongylus vitrinus* | A |
| *Trich ris globulosa* | H,Sn,SE,A |
| *Trichuris ovis* | H,Sn |
| | |
| *Avitellina* sp. | H |
| *Moniezia expansa* | H |
| *Stilesia hepatica* | Sn,Ss |
| | |
| *Fasciola hepatica* | H,D,Ss,K,A,M |
| *Paramphistomum microbothrium* | H,D,Sn,M |
| | |
| Occasional | |
| *Cooperia pectinata* | H,A |
| *Cooperia punctata* | H,A |
| | |
| *Fasciola gigantica* | NT,L,E |
| *Schistosoma mattheei* | NT,L,E |

TABLE 28 Definitive, occasional and accidental helminth parasites of cattle and their distribution in the RSA according to climate. For distribution code see Fig. 9

| Helminth species | Distribution |
|---|---|
| Definitive | |
| *Bunostomum phlebotomum* | H,L,D,E,SE |
| *Cooperia pectinata* | NT,H,D,E,SE,A,Sn,W |
| *Cooperia punctata* | NT,H,D,E,SE,A,Sn,W |
| *Dictyocaulus viviparus* | H,D |
| *Haemonchus placei* | NT,H,L,D,E,SE,Sn,W |
| *Nematodirus helvetianus* | E |
| *Oesophagostomum radiatum* | NT,H,D,E,SE,Sn,W |
| *Ostertagia ostertagi* | A,M,Ss,K |
| *Toxocara vitulorum* | H,E |
| | |
| *Moniezia benedeni* | NT,H,Sn |
| | |
| *Fasciola gigantica* | NT,L,E,SE |
| *Fasciola hepatica* | H,D,Ss,K |
| *Paramphistomum microbothrium* | NT,H,D,E,SE,Sn |
| *Schistosoma mattheei* | NT,L,E |
| | |
| Occasional | |
| *Haemonchus contortus* | H |
| *Nematodirus spathiger* | |
| *Strongyloides papillosus* | H |
| *Trichostrongylus axei* | H |
| *Trichostrongylus colubriformis* | NT,H |
| *Trichostrongylus falculatus* | NT |
| | |
| *Stilesia hepatica* | |
| | |
| Accidental | |
| *Cooperioides hamiltoni* | NT,L,E |
| *Impalaia tuberculata* | NT,L,E |
| *Longistrongylus sabie* | NT,L |
| *Ostertagia circumcincta* | |

*Fasciola hepatica* (Ross, 1966) are definitive parasites of cattle.

Although *Strongyloides papillosus* is listed as an occasional parasite it may well be a definitive parasite adapted to transmammary trans= mission with adult worms being found only in young calves. A similar situation exists with *Toxocara vitulorum* which is a definitive cattle parasite occurring in cattle and buffalo (Round, 1968). Transmammary transmission also occurs (Warren, 1969) and adult *T. vitulorum* are usually found only in young calves.

The other parasites listed as occasional or accidental are those that have been encountered in cattle utilizing the same habitat as sheep or impala (Surveys 6 and 7).

The helminths of impala and blesbok and their distributions are listed in Tables 29 and 30. These check-lists for impala and blesbok are certainly not complete as few detailed studies from which these lists can be compiled have been conducted in these hosts.

The distribution of impala within the RSA (Ansell, 1971), corresponds closely to the climatological regions described as subtropical and semi-arid (NT), subtropical, warm and muggy except in mid-winter (L) and warm and moist (E) (Fig. 9). These regions plus the region designated warm, temperate and moist (SE) (Fig. 9) comprise the Southern Savanna Woodland biotic zone (Rautenbach, 1978). Blesbok are distributed mainly within the boundaries of the climatological regions described as having a warm, temperate monsoonal type of climate (D and H) (Ansell, 1971; Fig. 9). These regions very nearly constitute the Southern Savanna Grassland biotic zone (Rautenbach, 1978).

Taking these facts and the distribution of parasites according to climato= logical region (Tables 29 and 30) into consideration, it can be seen that impala and blesbok and hence their helminth parasites are confined within the respective biotic zones of the antelope. Within these zones, however, the distribution of the helminths is determined by climate.

Three definitive nematode parasites of impala or blesbok warrant discussion in that they are also listed as definitive parasites of sheep. *Haemonchus contortus* is a parasite of sheep in most parts of the world

TABLE 29 Definitive, occasional and accidental helminth parasites of impala and their distribution in the RSA according to climate. For distribution code see Fig. 9

| Helminth species | Distribution |
| --- | --- |
| Definitive | |
| *Cooperia fuelleborni* | NT,L,E |
| *Cooperia hungi* | NT,L,E |
| *Cooperioides hamiltoni* | NT,L,E |
| *Cooperioides hepaticae* | NT,L,E |
| *Gaigeria pachyscelis* | L,E |
| *Haemonchus bedfordi* | L,E |
| *Impalaia tuberculata* | NT,L,E |
| *Longistrongylus sabie* | NT,L |
| *Oesophagostomum columbianum* | NT,L |
| *Pneumostrongylus calcaratus* | L,E |
| *Strongyloides papillosus* | NT,L,E |
| *Trichostrongylus colubriformis* | NT,L,E |
| *Moniezia expansa* | NT |
| Occasional | |
| *Cooperia connochaeti* | L |
| *Haemonchus placei* | NT |
| *Trichostrongylus axei* | NT,E |
| *Trichostrongylus falculatus* | NT |
| *Moniezia benedeni* | L |
| *Stilesia hepatica* | L,E |
| Accidental | |
| *Bunostomum trigonocephalum* | L |
| *Fasciola gigantica* | NT |

TABLE 30 Definitive, occasional and accidental helminth parasites of blesbok and their distribution in the RSA according to climate. For distribution code see Fig. 9

| Helminth species | Distribution |
| --- | --- |
| Definitive | |
| *Cooperia hungi* | H |
| *Cooperia yoshidai* | H,E |
| *Dictyocaulus magnus* | H |
| *Haemonchus bedfordi* | H |
| *Haemonchus contortus* | NT,H |
| *Impalaia nudicollis* | NT,H |
| *Impalaia tuberculata* | H |
| *Longistrongylus albifrontis* | H |
| *Skrjabinema alata* | NT,H |
| *Trichostrongylus thomasi* | H |
| | |
| Occasional | |
| *Oesophagostomum columbianum* | H |
| *Trichostrongylus axei* | NT,H |
| *Trichostrongylus falculatus* | NT,H |
| | |
| *Avitellina* sp. | NT,H |
| | |
| Accidental | |
| *Agriostomum equidentatum* | H |

(Levine, 1968), and its recovery from a large number of antelope species (Round, 1968) and its presence in many blesbok in the present surveys confirm its definitive nature in these animals. I suggest that this is a new association, that *H. contortus* evolved in sheep and that its presence in wild ruminants is due to the introduction of sheep into the habita of these animals and to the large numbers of eggs laid by this worm (Gordon, 1948, 1950) thus exposing sympatric species to infestation. Furthermore many antelope have definitive *Haemonchus* spp. of their own (Round, 1968) and it seems unlikely that *H. contortus* would evolve in sheep and at the same time in a large number of other hosts.

*Gaigeria pachyscelis* has been recovered from sheep and goats in Africa and India although Ortlepp (1937) concluded that it was comparatively rare in India. It has been found also in a number of antelope in Africa, in the African buffalo (Round, 1968) and in a single Indian antelope that had recently been imported into the then Union of South Africa (Ortlepp, 1937). In sheep in the RSA the distribution of this parasite is confined to the semi-arid north-western regions (Ortlepp, 1937), while in impala (Heinichen, 1973) and blue wildebeest (Horak: Unpublished data) it is found in the sub-tropical eastern regions of Natal and the Transvaal. These regions have never been extensively used for sheep farming and this may explain why *G. pachyscelis* has not been recovered from sheep in these areas. This parasite, even in small numbers, is highly pathogenic for sheep (Hart & Wagner, 1971) and I suggest that, although the association is definitive, it is a new association and that an antelope is the original host.

The fact that *Oesophagostomum columbianum* occurs in sheep in the RSA (Barrow, 1964; Viljoen, 1964), and also in Australia (Gordon, 1950), where there are no antelope to sustain it, confirms that it is a definitive parasite of these animals. However, I consider the association to be of recent origin. Infestation in sheep frequently results in considerable reaction in the gut wall which may give rise to caseous or even calcified nodules (Horak & Clark, 1966). This does not signify a well-adapted host-parasite relationship, while I have seldom seen even mild reactions in infested impala, which I also consider to be definitive hosts.

All blesbok in Survey 11 were infested with *O. columbianum*, yet I classify it as an occasional parasite of this species as very few adult worms were recovered, indicating an inability to complete its life cycle. If, however, development was seasonally arrested in the fourth larval stage, a phenomenon previously only suggested for this nematode (Gordon, 1952, cited by Michel, 1974), and not because it was in an occasional host, future observations may well demonstrate *O. columbianum* to be a definitive parasite of blesbok.

The *Trichostrongylus colubriformis* listed as a definitive parasite of impala, and recovered from these animals both near Boekenhout and Pafuri, is of the variety with markedly concave spicules with short terminal hooks, and may be a separate species as discussed earlier (see p. 12). *Trichostrongylus falculatus* is considered an occasional parasite of impala as not all animals near Boekenhout were infested and the worm burdens in those that were infested were not large. In addition it was not recovered from impala near Pafuri (Survey 9) or from Zululand (Heinichen, 1973). The same applies to blesbok, for the animals that were infested at Lunsklip (Survey 10) had only small burdens, and at Badplaas (Survey 11) only two animals were infested, while a springbok in the same reserve harboured a large burden of this parasite.

*Haemonchus placei* probably evolved with cattle breeds of the species *Bos indicus* and is encountered in cattle of this species particularly in parts of the world where the climate is hot and moist (Soulsby, 1968; Levine, 1968). Its presence in nearly all impala in Survey 8 is a result of their sharing their habitat with cattle for many years rather than a definitive association. Furthermore, although larval burdens were high in impala, few adult worms were recovered, thus implying an occasional rather than a definitive association.

Cestodes of the genus *Avitellina* have been recovered from blesbok near Pretoria (Horak, 1978d) and at Lunsklip. Their lengths even when mature segments were present, rarely exceeded 100 mm in buck at either locality compared with 1,0 m or more in the sheep near Tonteldoos (Survey 5) and hence they can be considered no more than occasional parasites of blesbok.

The presence of a single *Agriostomum equidentatum*, a parasite of springbok (Mönnig, 1929), in only one blesbok in Survey 11 is an example of an accidental association resulting from the sympatry of blesbok and springbok in a comparatively small reserve at Badplaas. The recovery of

*Bunostomum trigonocephalum*, a hook worm of sheep, from impala near Pafuri (Survey 9) is not as easy to explain. There were no sheep to serve as a reservoir of infestation, but the facts that only four worms were recovered and that this parasite has not been recovered from impala before both point to an accidental association, with some other antelope possibly serving as a reservoir of infestation.

The geographical distribution of parasites given in each of the check-lists must be regarded as incomplete because of the absence of detailed survey records from many regions of the RSA. In this regard the recovery of *Ostertagia circumcincta* from sheep at Tonteldoos (Survey 5) is interesting. This is the first time that this parasite has been recovered from sheep on dry-land pasture on the Transvaal Highveld, and although the numbers recovered were not large enough to warrant inclusion of this region in the geographic distribution of *O. circumcincta*, future observations may determine that it has become well-established there.

The role of man-created environments in the distribution of parasites must also be considered. These have resulted in isolated parasite populations atypical of the region concerned. Thus irrigated lucerne pastures in the Karoo are ideal for the free-living stages of *Haemonchus contortus*, a parasite encountered normally only in small numbers in parts of this region (Viljoen, 1969). Likewise the irrigated pastures at Hennops River and at Diepsloot, a nearby farm, created conditions suitable for *Ostertagia circumcincta* and *O. ostertagi*, parasites respectively of sheep and cattle and usually unknown in this region. Such localised foci of exotic parasites would not be recorded on a map illustrating geographic distribution, but their existence may nevertheless be of considerable importance from the control point of view in the locality concerned.

A knowledge of the geographic distribution and seasonal occurrence of helminths is of practical importance when devising control programmes for a particular region. Thus the programmes suggested by Barrow (1964) and Rossiter (1964) for the control of nematodes in sheep in the eastern Cape Province differ from that used by Horak *et al.* (1976) in sheep on the Transvaal Highveld. Data on both aspects still have to be gathered from such important regions as the western Cape Province, Natal, the Orange Free State and the Transvaal Lowveld before control programmes covering the entire country can be devised.

## *THE SEASONAL INCIDENCE OF THE MAJOR NEMATODE GENERA*

Certain nematodes, because of their numerical preponderance or presence in a large percentage of survey animals, can be considered of major importance. These nematodes either belong to particular genera such as *Haemonchus*, *Trichostrongylus* or *Oesophagostomum* or can be grouped because of morphological and organ preference similarities as is the case with the *Ostertagia/Longistrongylus* group in the abomasum and the *Cooperia/Cooperioides/Impalaia* group in the small intestine. Because all the seasonal incidence surveys were conducted in regions of the Transvaal where frost is possible during winter the seasonal occurrence of worms within each genus or group can be compared and an overall picture for that genus or group be obtained. As the seasonal incidence of parasitic nematodes is closely coupled to the ecology of their free-living stages this topic will also be discussed for each of the major genera. Before this is done, however, a few general considerations are worthy of mention.

Faecal deposition by sheep, even in a restricted camp, is not random (Crofton, 1954; Donald & Leslie, 1969). The position of a flock in a pasture would appear to be related to the distribution of faeces; it will rarely graze the area which had shown the highest concentration of faeces the previous day, but it will eventually return to the area previously contaminated (Crofton, 1954). If this occurs in less than five to seven days the chances of infestation will not be great as few infective larvae will have developed. If it occurs thereafter the severity of infestation will depend on the degree of larval development and survival of infective larvae.

The role of the cattle dungpat acting both as a reservoir when moist and then as a prison for infective larvae when the crust dries out (Reinecke, 1960a) must be considered. The disintegration of these pats by dungbeetles with consequent death or burial of larvae before reaching infectivity (Reinecke 1960a; Bryan, 1973; Fincher, 1975) is an important factor in the epizootiology of nematodes of cattle.

Climate plays a major role in the development and survival of the free-living stages (Levine, 1963). When it is unfavourable develop= ment may not take place, or be delayed for several weeks, or the larvae which do develop may not survive for long. When favourable, development may be rapid and survival for many months be possible (Gibson & Everett, 1967, 1972, 1976; Anderson, 1972; Southcott *et al.*, 1976). Although temperatures may be too low for larval development they may, however, ensure the survival of larvae already present (Levine & Andersen, 1973).

The micro-climate within any habitat is also of considerable importance. It has been demonstrated that soil temperature is considerably higher than air temperature when recorded below a covering of snow (Gibson, 1966) or below 70 to 100 mm of grass (Andersen *et al.*, 1970), while Okon & Enyenihi (1977) have shown that grass temperature can be below air temperature. Reinecke (1960b) found that during the summer months in the north-western Cape Province more larvae developed to the infective stage in cattle dung protected from the sun than in that exposed to direct sunlight.

The slower development of larvae in winter faecal depositions may coincide with the more rapid development of larvae in spring depositions so that large numbers of larvae become infective at the same time and is an important consideration in the epizootiology of helmintho= sis. Furthermore larvae which have survived on pasture during winter or for prolonged spells after the removal of sheep may serve as a source of infestation for young lambs (Thomas & Boag, 1968, 1972; Donald & Waller, 1973), or freshly introduced sheep.

Once ingested the establishment of infestation is affected by factors such as the host's age (Herlich, 1960; Viljoen, 1969; Gordon, 1973), sex (Dobson, 1964; Bawden, 1969), nutritional status (Bawden, 1969), or state of resistance (Donald *et al.*, 1964) and also by the rate of flow of ingesta (Bawden, 1970), presence of other parasites in the preferred site (Reinecke, 1974), or the host specificity of the parasite (Southcott & Barger, 1975).

Rapid development within the host coupled with rapid development on pasture will lead to short generation intervals (Donald & Waller, 1973), whereas delayed development on pasture or arrested development in the host may result in a single generation annually (Connan, 1971; Waller & Thomas, 1975).

Arrested development, a phenomenon encountered in all the surveys, will here be briefly discussed as it affects each of the major genera, and in greater detail at a later stage.

*Haemonchus* spp.

Worms of this genus were present in ruminants in each of the surveys and their seasonal incidence is graphically illustrated in Fig. 10.

The sheep in Surveys 3, 4 and 5 and blesbok in Survey 10 were infested with *H. contortus*. Peak burdens were recovered from February to April or May in sheep and during February, September and October in blesbok. Burdens were at a low level from June or July until November or December in sheep and from April to July in blesbok.

The cattle in Surveys 6 and 7 and impala in Survey 8 were infested with *H. placei*. Peak burdens in Survey 6 were recovered during June and July with low numbers present in January, October and November. In Survey 7 the greatest numbers of worms were present in January and December and none were recovered from August to October. The impala harboured peak burdens from April to October and few worms during February and December.

Despite this fairly considerable variation certain constant features emerge. In Surveys 3 to 7, in which tracer animals were used, few larvae were available on pasture for some time during the period July to October. With the possible exception of Survey 10 a large proportion of the worm burden was arrested in the fourth larval stage from May to September, and adult worms always outnumbered fourth stage larvae during January and frequently also during November and December.

Gordon (1948) showed that optimal conditions for the free-living stages of *H. contortus* were monthly rainfall in excess of 50,8 mm (2 in) and mean atmospheric temperatures above 17,7$^{o}$C (63,9$^{o}$F). Silverman & Campbell (1959) and Viljoen (1964), however, have shown that development can proceed at lower temperatures. Levine (1963) records the tempera= ture limits for optimum development as mean monthly mean temperatures of 15 to 37$^{o}$C and monthly rainfall as in excess of 50 mm. But Viljoen (1969), working in the Karoo, felt that it was more realistic to regard 25 mm as the minimum requirement. This variation in the

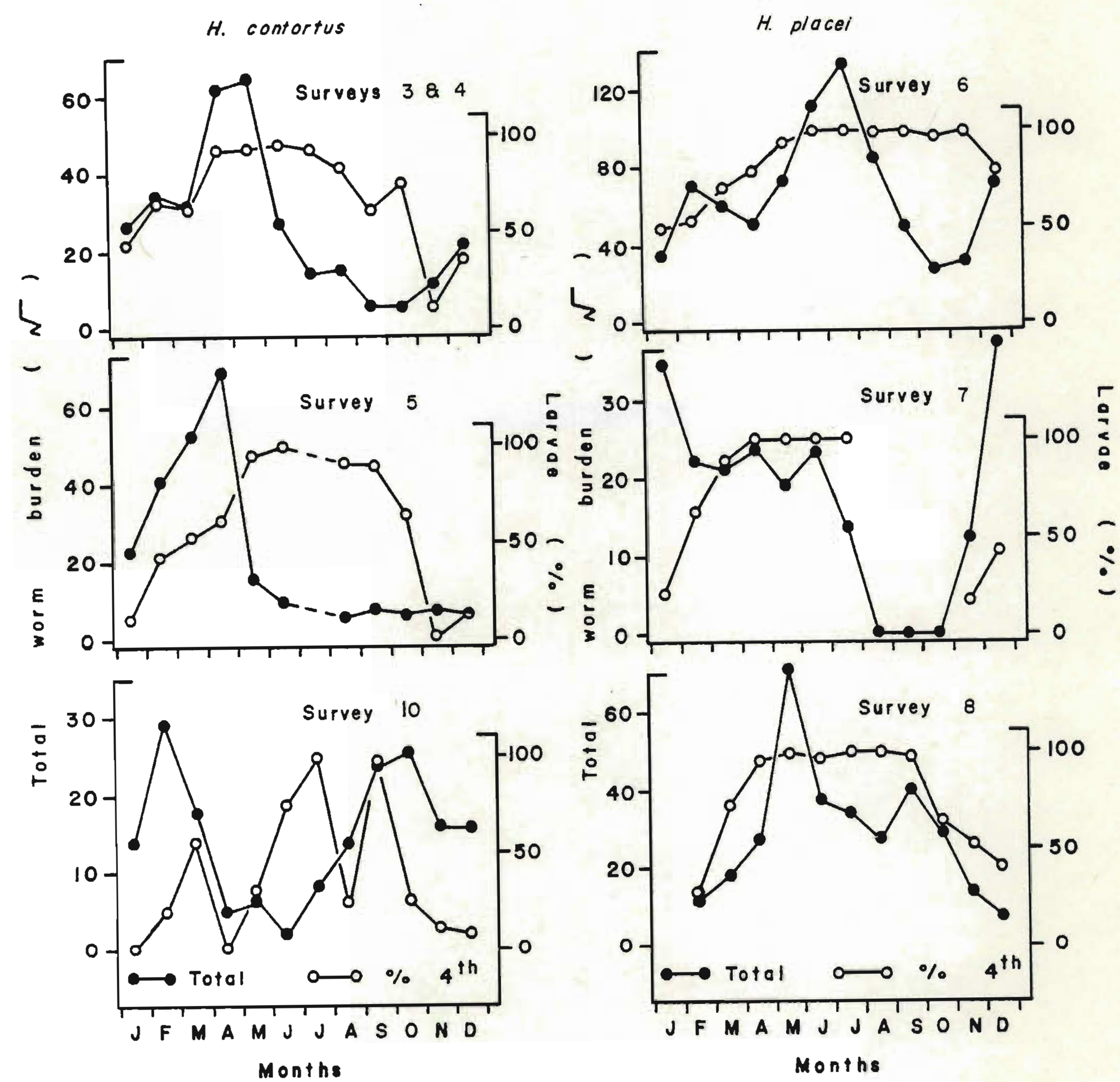



Fig. 10 The seasonal incidence of *Haemonchus* spp. in sheep, cattle, impala and blesbok slaughtered in surveys conducted in the Transvaal. Surveys 3, 4 and 5 - sheep, Surveys 6 and 7 - cattle, Survey 8 - impala, Survey 10 - blesbok

requirements of the free-living stages may, however, be the result of ecological selection (Crofton, Whitlock & Glazer, 1965) with various strains having different requirements.

In each of the survey areas temperature and rainfall or irrigation were probably suitable from October or November to March or April. Yet the relationships between larval development and adequate temperature and moisture are reflected only in the December to April burdens in Surveys 3, 4 and 7, January to April burdens in Survey 5, December burden of Survey 6, and November to March burdens of Survey 10. At other times burdens were either higher or lower than environ= mental conditions seemed to dictate. Possible reasons for these differences will be suggested below.

At Armidale in Australia Southcott *et al.* (1976) found that contamination of the pasture with eggs from December to January was rapidly trans= lated to peak numbers of larvae while contamination in autumn and spring was less effective. Judging by differential faecal worm egg counts that were done on infested animals running with the present survey animals, *Haemonchus* spp. eggs were being deposited on pasture in fair numbers during the period October to April and it was particularly the eggs deposited in spring that were not being effectively translated to larvae. The inability of larvae to survive on pasture during spring is probably due to climatological stresses as suggested by Southcott *et al.* (1976). The most important of these stresses in the Transvaal would seem to be solar radiation because of poor pasture cover at that time.

Thomas (1967), working near Ermelo on the Transvaal Highveld, has commented on the role played by moisture in the survival of infective larvae, pasture infestation dropping markedly within two to three weeks of the onset of dry conditions. The results of Survey 5, conducted in an area fairly close and similar to the Ermelo district, would seem to confirm this observation, but in Surveys 3 and 4, where moisture was regularly supplied, cold would seem to have been responsible for the decline in pasture infestation.

Southcott *et al.* (1976) demonstrated that *H. contortus* larvae could overwinter on pasture at Armidale, Australia, but that this occurred in substantial numbers only if the pastures were contaminated during January and February. At Weybridge in the south of England, Gibson

& Everett (1976) found that infective larvae which developed from April to June survived for a shorter period of time than those that developed from July to September. The latter larvae were able to overwinter but all of them disappeared during the following spring.

Larval availability can only be accurately determined in those surveys in which tracer animals were used and the findings in Surveys 3 and 4, 5 and 7 indicate that very few or no larvae over-wintered on pasture. The difference between this result and those obtained at Armidale and Weybridge can be explained by the environmen= tal stress to which the larvae in the South African surveys were subjected during winter. Not only is the pasture cover poor, but daily atmospheric temperature variation is at its greatest and evaporation and radiation are high because of the usually cloudless skies. In support of the latter hypothesis, at Hennops River where regular irrigation was supplied, the pasture cover was greater and winter temperatures were higher than at Tonteldoos, larger numbers of larvae were recovered from tracer lambs grazed during winter than at the latter venue.

The important role played by the cattle dungpat in the survival of larvae is well illustrated by the results of Surveys 6 and 7. In Survey 7 the last substantial rainfall was recorded during April and yet comparatively large numbers of larvae were recovered from tracers until June, while in Survey 6 the regular supply of moisture ensured that large numbers of larvae were available until August and over= wintering of larvae on the pastures probably occurred in this survey. These observations confirm the findings of Reinecke (1960b) who recorded that *H. placei* larvae could survive for 105 days in the dungpat and 41 days on the surrounding grazing during autumn in the semi-arid north-western Cape Province. In Survey 7 the dungpat probably eventually became a prison for the larvae as its surface was baked by the sun while in Survey 6 it served as an effective reservoir (Reinecke, 1960a) as it was regularly moistened.

The striking difference between the burdens of *H. placei* in cattle in Survey 7 and impala in Survey 8 have been previously mentioned. These animals grazed the same area albeit in different years and while the highest worm counts in cattle were recorded during January and December the lowest in impala were recorded during February and

December. This may be due either to the presence of adult *Longistrongylus sabie* in the abomasa of impala from November onwards, these worms thus occupying the preferred site of *Haemonchus placei* (Reinecke, 1974), or that *H. placei* is not a definitive parasite of impala and hence, although larval burdens may be large, few adult worms develop.

*Ostertagia* spp. and *Longistrongylus sabie*

*Ostertagia* spp. were present in each of the surveys conducted in sheep, while *Longistrongylus sabie* was recovered from cattle and impala near Boekenhout. The mean worm burdens of these species are graphically reproduced in Fig. 11.

Muller (1968) stated that the temperature and moisture requirements of *Ostertagia* spp. are similar to those of *Trichostrongylus* spp. He worked at Outeniqua, in the south-western Cape Province, where the greatest numbers are recovered during the cooler, moister months from autumn to spring, and the warm summers with the possibility of high evaporation are detrimental to the free-living stages of both species. In Australia Anderson (1972) and Southcott *et al.* (1976) found that larvae of *Ostertagia* spp. were abundant on pasture from June to October when the mean maximun temperature was 15,5°C.

At Hennops River larvae were available on pasture in greater numbers from autumn to spring than at other times (Surveys 3 and 4) con= firming the observations of Muller (1968), Anderson (1972) and Southcott *et al.* (1976). A reasonably similar pattern was observed at Tonteldoos (Survey 5), but worm burdens were very low, as well as in impala near Boekenhout where, however, the animals were continuously exposed to infestation and exact times of larval acquisition could not be determined.

There is a considerable difference between pasture contamination patterns in warm and cold climates. Southcott *et al.* (1976) demonstra= ted that at Armidale in Australia, where winters are not too severe, autumn contamination of pastures with *Ostertagia* spp. eggs resulted in peak larval recoveries in late winter and early spring, while spring or summer contamination never resulted in high larval numbers. At Weybridge in southern England where winters are cold Gibson & Everett (1972) found that development time on the pasture was long and larval

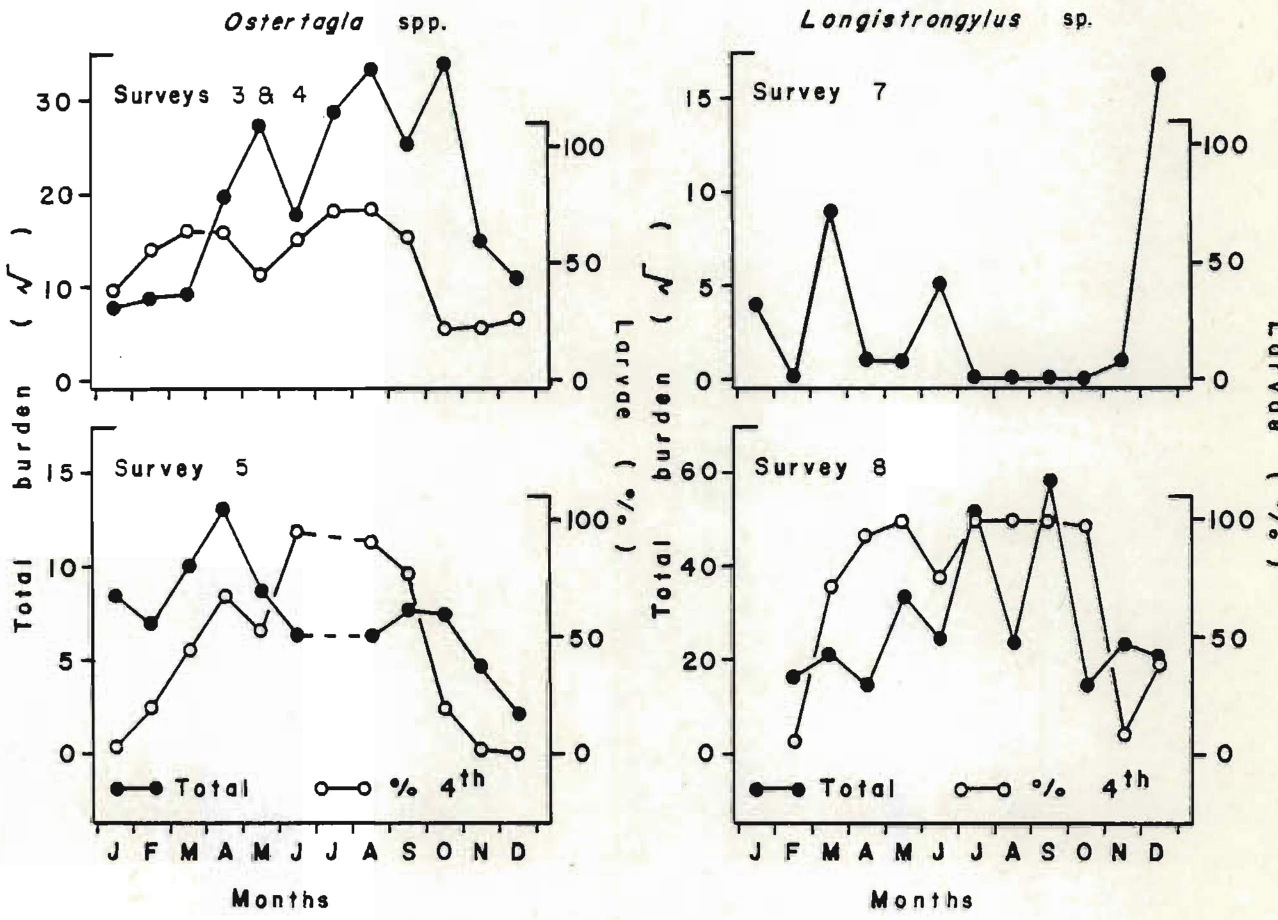



Fig. 11 The seasonal incidence of *Ostertagia* spp. in sheep and *Longistrongylus sabie* in impala and cattle slaughtered in surveys conducted in the Transvaal. Surveys 3, 4 and 5 - sheep, Survey 7 - cattle, Survey 8 - impala

yields small from winter to early spring, while during the rest of the year development was rapid and larval yields were high. Basically similar findings were recorded by Boag & Thomas (1970) in north-eastern England. Thus in warm climates *Ostertagia* spp. produces a winter and spring infestation while in cold climates it produces a summer and autumn infestation. The findings at Hennops River confirm this observation in that the climate was warm and peak burdens were present in winter and spring.

Gibson & Everett (1972) demonstrated that *O. circumcincta* could overwinter on pasture at Weybridge and that this infestation survived until summer. At Armidale Southcott *et al.* (1976) found that although *Ostertagia* spp. appeared capable of development on pasture throughout the year and survival was good, the larvae rapidly declined from October to December. Thus in England overwintered larvae disappeared in summer yet newly developed larvae could survive, while in Australia both overwintered and newly developed larvae declined during spring and summer. At Hennops River and Tonteldoos *Ostertagia* spp. larvae developed to infectivity on pasture during autumn to spring and could probably overwinter, but declined rapidly during November and December (Surveys 3, 4 and 5). The environmental stresses of tempera= ture, high evaporation and exposure to direct sunlight were probably responsible for their disappearance.

At both Hennops River and Tonteldoos a fairly large percentage of the worm burden was arrested in the fourth larval stage from February or March until September. At both localities a temporary decline in the percentage of arrested larvae took place during May or June.

Although *L. sabie*, as discussed earlier, is in many respects similar to *Ostertagia* spp., its epizootiology differs markedly from that of the latter genus in sheep in the Transvaal. At Hennops River the greatest mean total numbers of *Ostertagia* spp. larvae were available on pasture from April to October and the greatest mean numbers of adult worms were recovered during May and from July to October (Surveys 3 and 4). Near Boekenhout the largest numbers of adult *L. sabie* were recovered from November to February (Survey 8) and infestation on pasture was available from November to June if one considers the results obtained from the tracer calves (Survey 7).

Thus *Ostertagia* spp. produced an autumn to spring infestation at Hennops River whereas near Boekenhout *L. sabie* produced a summer to early winter infestation. At Hennops River a fairly large per= centage of the worm burden was arrested in the fourth larval stage during winter (Surveys 3 and 4), to avoid exposure of the free-living stages to the external cold temperature, while near Boekenhout (Survey 9), where the winters were considerably warmer, arrested development was essential to survive during the dry winter months.

In many respects the epizootiology of *L. sabie* near Boekenhout closely resembles that of *Ostertagia ostertagi* in calves near Glasgow, Scotland (Anderson *et al.*, 1965). At both localities in= fective larvae are available in summer and autumn, adult worms are present in summer, and infestation overwinters in the host, as arrested fourth stage larvae. The reason for overwintering in the host, however, differs. In Scotland it is to ensure survival during a period of considerable cold; near Boekenhout during a time of drought.

*Trichostrongylus* spp.

Worms of this genus were present in each of the surveys and their seasonal fluctuations are graphically illustrated in Fig. 12.

The magnitude of the worm burdens encountered in the present surveys is a clear indication that the Transvaal climate is not ideal for the survival of free-living stages of *Trichostrongylus* spp. With the single exception of the worm burden of a single impala (Table 17), mean burdens did not exceed 3 000 worms and usually not 1 000 worms. In contrast the burdens recovered by Barrow (1964), Viljoen (1964) and Snijders *et al.* (1971) from sheep in the Cape Province usually exceeded 5 000 worms and frequently 10 000 worms.

In the surveys conducted in sheep and cattle on the Transvaal Highveld (Surveys 3 to 6) a major peak of infestation occurred during the period March to June, while infestation was at its lowest during September or October, picked up slightly for one month and dropped to a low level during December to February. In the northern Transvaal infestation in cattle and blesbok was at its highest during December (Surveys 7 and 10), while no clear pattern emerged in impala (Survey 8).

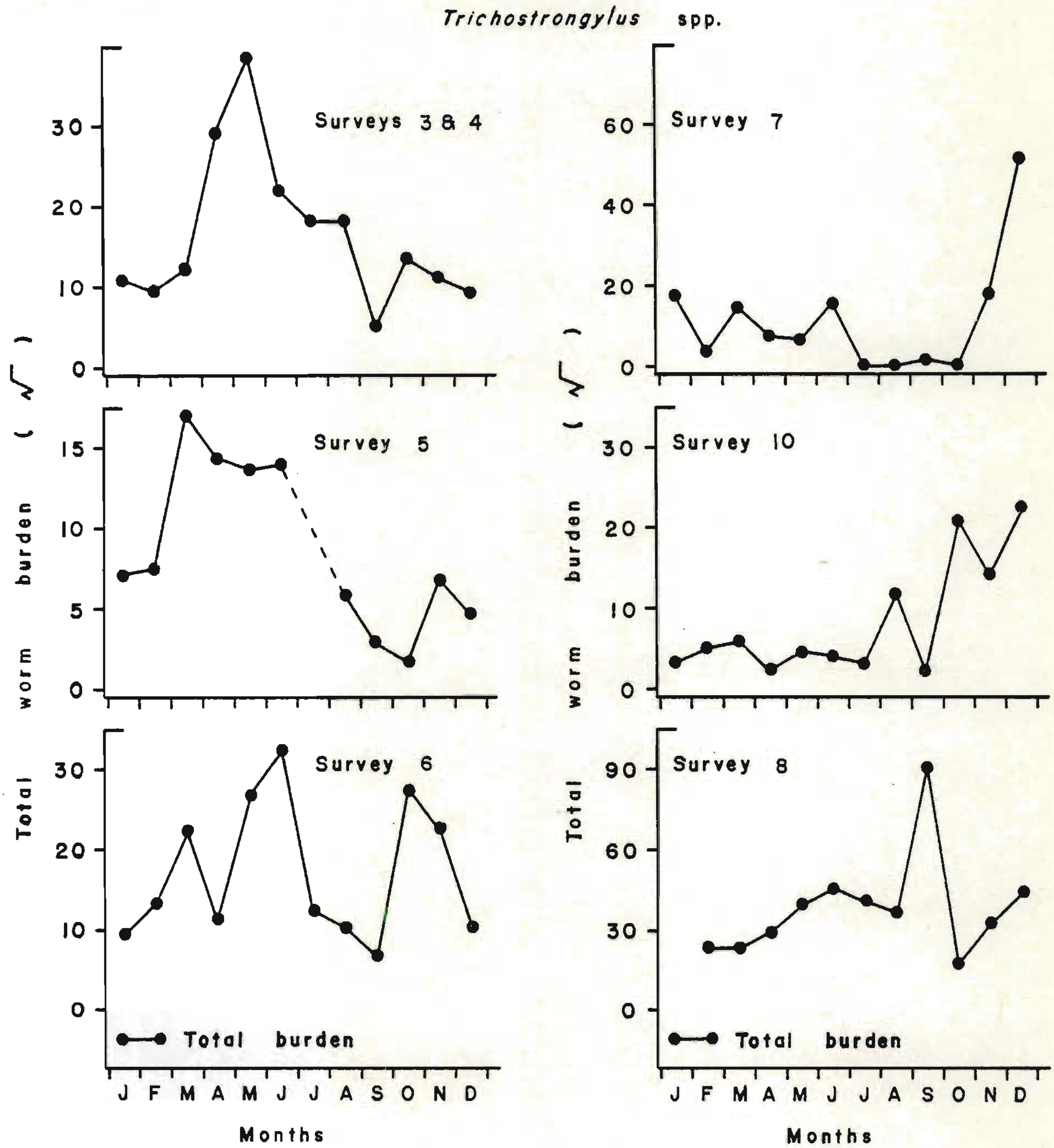



Fig. 12 The seasonal incidence of *Trichostrongylus* spp. in sheep, cattle, impala and blesbok slaughtered in surveys conducted in the Transvaal. Surveys 3, 4 and 5 - sheep, Surveys 6 and 7 - cattle, Survey 8 - impala, Survey 10 - blesbok

Roberts *et al.* (1952) stated that the optimal requirements for the free-living stages of *Trichostrongylus* spp. were mean maximum temperatures from 12,8 to 18,3°C (55 to 65°F) and monthly rainfall of 76,2 mm (3 in) or more. While agreeing with the temperature requirements Gordon (1953) concluded that a monthly rainfall of 50,8 mm (2 in) or more was adequate as did Levine (1963), who recorded the temperature limits for optimum development of the free-living stages as being mean monthly mean temperatures of 6 to 20°C.

The survey conducted in sheep in the Karoo by Viljoen (1969) indicated that the environmental requirements of various *Trichostrongylus* spp. may differ. In contrast with the findings of Gordon (1953) and Levine (1963) he found that in the case of *T. falculatus* a monthly rainfall below 25 mm was still adequate provided a good fall occurred in autumn and the winter was cold. The findings of Southcott *et al.* (1976) confirm these differences in that they found peak pasture larval availability for *Trichostrongylus* spp. parasitic in the small intestines during March, and for the abomasal parasite *T. axei* during September.

The seasonal fluctuations in infestation in Surveys 3 to 6 can probably be explained in relation to the temperature requirements of the free-living stages. Infestation during January and February was at a low level because of summer temperatures, increasing thereafter as the late summer and autumn temperatures favoured the free-living stages. During winter development slowed down or ceased and available infestation died off, resulting in very low worm burdens in September or October. The rise in temperature during October or November resulted in a slight increase in available larvae but thereafter summer temperatures became too warm and infestation declined.

The same arguments, however, cannot be used to explain findings in cattle near Boekenhout (Survey 7). Slaughter in this survey commenced during March 1976 (Table 15), and small numbers of *T. colubriformis* and *T. falculatus* were recovered until June, whereafter both temperature and drought prevented further larval development or escape of larvae from dungpats. Although temperatures rose during spring no larvae became available until after the rain in October and considerably more rain in November, resulting in the highest worm burdens in the calves slaughtered on 1 December 1976. This infestation could be of threefold origin, developing either from embryonated eggs which in the case of *Trichostrongylus* spp. are resistant to adverse conditions (Mönnig, 1930) and have overwintered, or from infective larvae trapped in the dungpats and unable to escape because of lack of moisture, or from newly deposited eggs. Despite further rainfall, summer temperatures were probably too high and worm burdens declined markedly thereafter.

It is quite probable that regular irrigation at Hennops River prevented cattle dungpats from acting as prisons as they would be kept moist and larvae would not become trapped (Reinecke, 1960a). If this indeed was so it would explain the difference in infestation patterns in cattle at Hennops River (Survey 6) and Boekenhout (Survey 7).

Gibson (1966) and Gibson & Everett (1967), working at Weybridge in the south of England, found that larvae developing from *T. colubri=formis* eggs placed outside during March and April 1963 did not survive for long although they had in the previous year. Larvae developing from eggs deposited from May to September were capable of overwinter=ing but disappeared the following spring. These findings are corroborative evidence of the short-lived spring rise in infestation encountered in Surveys 3 to 7.

It is apparent that infestation in blesbok at Lunsklip (Survey 10) increased from August to December and declined markedly thereafter. This rise could have been due to rainfall, but as no data are available and these animals and impala near Boekenhout (Survey 8) were continuously exposed to infestation, it is difficult to draw conclusions on the seasonal availability of larvae.

*Cooperia* spp., *Cooperioides* spp. and *Impalaia* spp.

The mean monthly burdens of these species in animals in Surveys 5 to 8 and 10 are graphically reproduced in Fig. 13.

Acquisition of *Cooperia* spp. infestation by tracer lambs in Survey 5 and tracer cattle in Surveys 6 and 7 was reasonably similar, and although not graphically illustrated, acquisition of *I. tuberculata* by cattle in Survey 7 at times closely resembled that of *Cooperia* spp.

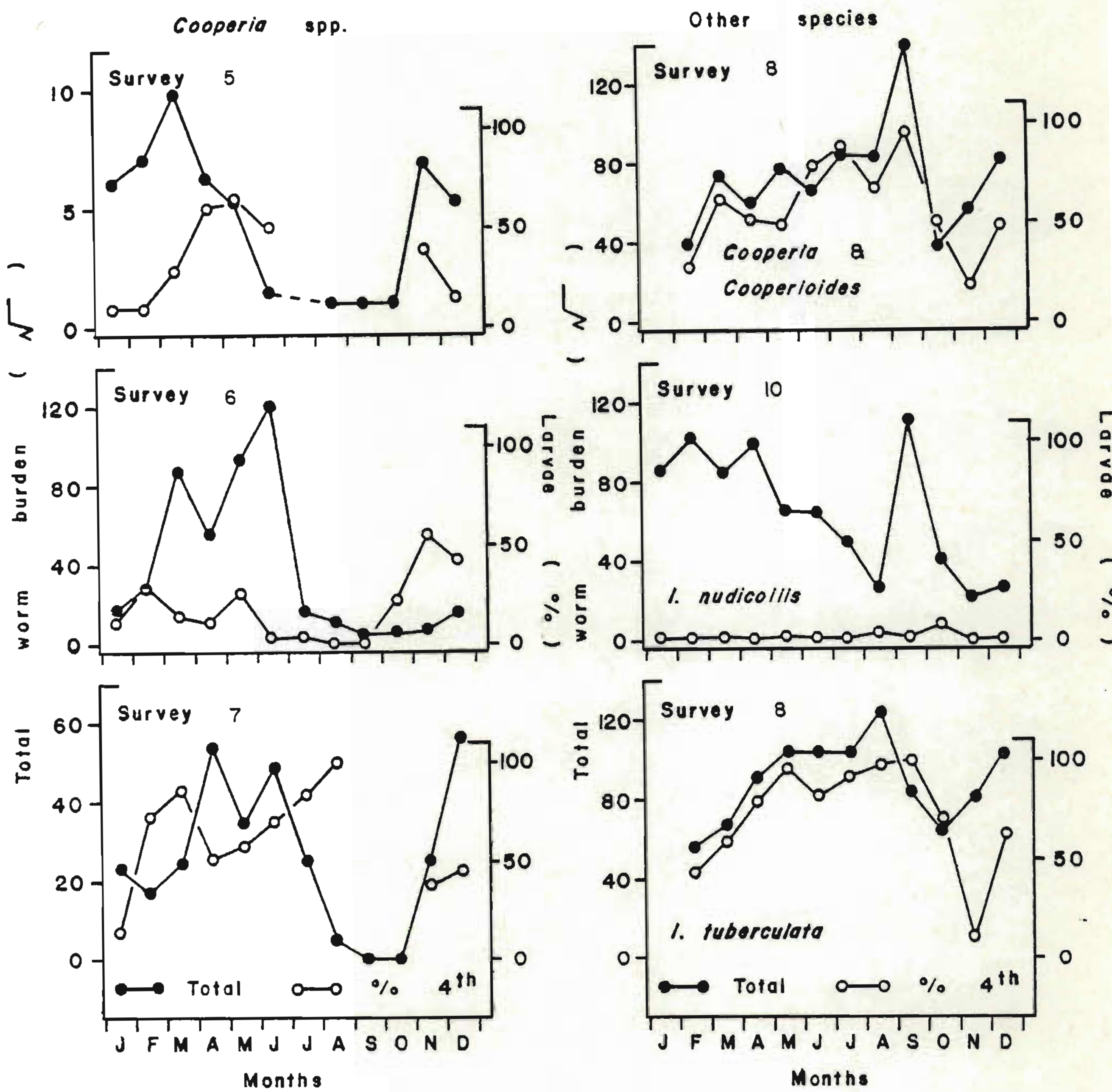



Fig. 13 The seasonal incidence of *Cooperia* spp. in sheep and cattle, *Cooperia* sp., *Cooperioides* spp. and *Impalaia* sp. in impala and *Impalaia* sp. in blesbok slaughtered in surveys conducted in the Transvaal. Survey 5 - sheep, Surveys 6 and 7 - cattle, Survey 8 - impala, Survey 10 - blesbok

by the same animals (Table 15). Worm burdens increased from January or February and infestation was acquired until May by lambs and until June by cattle, followed by a marked decline and very small worm burdens for a period of three to five months. A marked increase in worm burden during November was evident in the lambs, and in cattle in Survey 7, and a slight increase during December in cattle in Survey 6. More than 50 per cent of total worm burdens consisted of arrested fourth stage larvae, from April to June in lambs, in November in calves in Survey 6 and from February to August in calves in Survey 7.

The *Cooperia*/*Cooperioides* spp. and *Impalaia tuberculata* burdens of impala in Survey 8 followed generally similar patterns to each other, rising from February to a peak in either September or August, followed by a decline to October and an increase thereafter. More than 45 per cent of total worm burdens from March to October and during December consisted of fourth stage larvae, the greatest proportion of larvae being present during September. The decline in total worm burden in October was accompanied by a decline in the proportion of fourth stage larvae and a rise in the actual number of adult worms present.

With the exception of September, burdens of *I. nudicollis* in blesbok in Survey 10 declined erratically from January to December. Very few fourth stage larvae were recovered from these animals.

The two most common *Cooperia* spp. of cattle are probably *C. oncophora* and *C. pectinata*. The former is a parasite of colder climes and is found in the United Kingdom (Anderson *et al.*, 1965), Canada (Smith, 1974), the northern states of the United States of America (Levine, 1968), New Zealand (Brunsdon, 1972) and cooler regions of Australia (Southcott & Barger, 1975). The latter species prefers warmth and is present in the southern states of the United States (Levine, 1968), the summer rainfall regions of the RSA (Reinecke, 1960; Surveys 6 and 7) and the warmer regions of Australia (Roberts *et al.*, 1952; Henderson & Kelly, 1978).

In England Michel *et al.* (1970a) have shown that after contamination of pasture with eggs of *C. oncophora* during May, infective larvae were able to survive until the following April. At Armidale, Australia Southcott & Barger (1975) found that the larvae of *C. oncophora* persisted on pasture for at least 24 weeks during summer and autumn.

Ecological studies done on the free-living stages of *C. pectinata* have usually been combined with observations on the free-living stages of the other cattle nematodes. Thus Roberts *et al.* (1952) in Queensland, Australia found that larvae of *Cooperia* spp. (*C. pectinata* and *C.punctata*) and *Oesophagostomum radiatum* could still be found in dungpats three months after exposure during the warmer seasons of the year. Reinecke (1960b), working in the semi-arid north-western Cape Province, found that the larvae of *Cooperia pectinata* were well adapted to extremes of heat and cold and to dessication. They persisted longer in dungpats and their surrounds than larvae of *Haemonchus placei*, *Bunostomum phlebotomum* and *Oesophagostomum radiatum*, and migrated and survived when no other species were found.

The findings at Hennops River (Survey 6) indicate that cold does play a role in the development or survival of *Cooperia* spp. on pasture. Regular irrigation should have supplied sufficient moisture for the free-living stages, yet a decline in infestation was evident in tracer calves slaughtered during August and September 1969 compared with that in calves examined in the previous months (Table 13). Unfortunately the survey was terminated in June 1970 at the height of infestation, hence no counts for the succeeding months are available.

Near Tonteldoos (Survey 5) and Boekenhout (Survey 7) both temperature and lack of rainfall probably accounted for the decline in available infestation. Yet at both these localities the free-living stages apparently survived on pasture during winter, judging from the rapid increase in infestation in tracer animals during November. The role of cattle dungpats in survival of infestation was probably important at both sites. (Cattle grazed with or before sheep near Tonteldoos as mentioned previously). Larvae were probably trapped in dungpats of which the crusts had become hard during the dry winter months (Reinecke, 1960a) and were then liberated in November and December after the first rainfall. Temperatures thereafter near Tonteldoos were probably suitable for development and survival, while near Boekenhout, with a considerably warmer summer, a marked decline in infestation was evident in January.

Near Tonteldoos and Boekenhout a fairly large proportion of the worm burdens consisted of fourth stage larvae, particularly during the cooler, drier months. A similar phenomenon was not evident at Hennops River (Survey 6), possibly because the regular supply of moisture during the winter months reduced the pressure to overwinter in the host and a non-inhibition prone strain was rapidly selected (Michel, Lancaster & Hong, 1973).

Acquisition of *Impalaia tuberculata* by cattle near Boekenhout (Survey 7, Table 15), although similar to that of *Cooperia* spp., differed markedly during January and February when no infestation was available, compared with a reduced level for *Cooperia* spp. Lack of infestation is confirmed by the worm burdens of impala, in which the lowest burdens of *Impalaia tuberculata* were recovered during February (Survey 8), indicating the absence of infective larvae on pasture. A remarkably similar pattern of infestation is evident for the *Cooperia*/*Cooperioides* complex in impala.

Combining the findings for the tracer cattle and sheep with those of continuously exposed impala I would suggest the following epizootiology for *Cooperia* spp., *Cooperioides* spp. and *Impalaia* spp. in the Transvaal: at elevated altitudes infective larvae are available from November to April, while in warmer areas they are present in November and December and from February or March to June or July.

Notable exceptions to this pattern were *Cooperia* spp. on irrigated pasture at Hennops River (Survey 6) where large numbers of larvae were available from March to June, and *Impalaia nudicollis* on natural pasture near Lunsklip (Survey 10) where in addition to larvae apparently being available from January to April large numbers were present during September.

The free-living stages can overwinter on pasture, resulting in available larvae after the first rainfall at the start of the following spring or summer. Adult worms account for the major portion of the worm burden from November to February or March, when they are superseded by arrested fourth stage larvae overwintering in the host because of the cold and dry external environment. {At Hennops River (Survey 6) and Lunsklip (Survey 10) arrested development did not occur}. During

October these larvae develop to adulthood, many larvae or adults being eliminated at the same time. The surviving adults contaminate the pastures with eggs, and these eggs and the overwintered free-living stages give rise to November infestations which rapidly mature in the host.

Although infestation of blesbok with *Impalaia nudicollis* during the first few months of the year agreed with the abovementioned observations I can give no reason for the erratically declining population there= after, other than that reduction of blesbok numbers similarly affected their worm burdens. The fact that only two blesbok were examined at each occasion may also account for the fluctuating nature of the results.

*Oesophagostomum* spp.

No worms of this genus were recovered from blesbok at Lunsklip (Survey 10), very few from sheep near Tonteldoos (Survey 5) and cattle at Hennops River (Survey 6), fair numbers from sheep at Hennops River (Surveys 3 and 4), impala near Boekenhout and Pafuri (Surveys 8 and 9) and blesbok at Badplaas (Survey 11), and reasonably large numbers from cattle near Boekenhout (Survey 7). Fig. 14 graphically illustrates the worm burdens of animals in Surveys 3, 4, 7 and 8.

Peak burdens of *O. columbianum* were recovered from sheep during April and May, while small burdens and large fluctuations made the determina= tion of seasonal prevalence in impala impossible. In cattle *O. radiatum* reached peak numbers from June to January. The apparent major peaks observed during August and January are coupled to six-week grazing periods as opposed to periods of four weeks for cattle slaughtered during other months of the survey.

Few critical experiments on the development and survival of *Oesophagostomum* spp. on pasture seem to have been conducted. Reinecke (1960b) found that infective larvae of *O. radiatum* could survive in the dungpat for 105 days during the autumn and winter months in the semi-arid north-western Cape Province, but for only 41 days on grass adjacent to the pat. Viljoen (1964) suggested that infective larvae of *O. columbianum* probably prefer cooler conditions and hence infesta= tion with fourth stage larvae increased in sheep in the Karoo from autumn

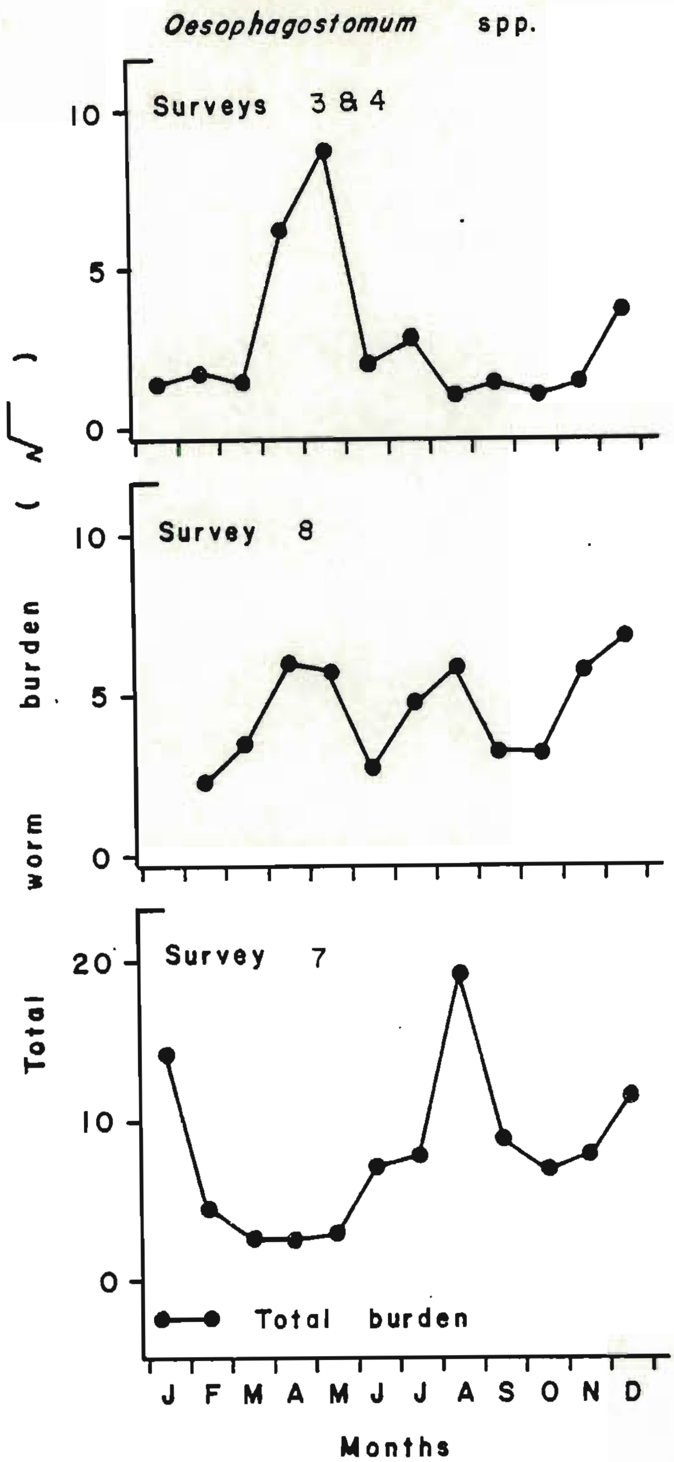



Fig. 14 The seasonal incidence of *Oesophagostomum* spp. recovered from sheep, cattle and impala slaughtered in surveys conducted in the Transvaal. Surveys 3 and 4 - sheep, Survey 7 - cattle, Survey 8 - impala

to spring. According to Thomas (1968), however, the free-living stages of *O. columbianum* are limited to the summer months, particularly during the high rainfall period on the Transvaal Highveld. This confirms Kates' (1950) observations near Washington in the United States of America. He found that the free-living stages of *O. columbianum* survive best under warm, moist conditions and poorly or not at all under warm and dry or cool and dry conditions. Snijders *et al.* (1971) demonstrated that infective larvae of *O. venulosum*, a parasite of sheep in the winter and non-seasonal rain= fall areas of the Cape Province, were present on pastures in peak num= bers during a period of high rainfall from September 1965 to January 1966.

The findings in the present surveys tend to confirm Viljoen's (1964) observation that infective larvae of *O. columbianum* prefer cooler conditions. It may also be that excessive moisture is detrimental to the survival of *O. columbianum* and *O. radiatum*. Peak burdens of *O. columbianum* were recovered from sheep slaughtered near Middelburg in the Karoo from May to August 1963, a period during which only 21,4 mm of rain fell (Viljoen, 1964). At Hennops River (Surveys 3 and 4), *O. columbianum* did not flourish on the pastures except for a brief spell during April and May, thus indicating that the amount of moisture supplied may have been excessive as well as that the free-living stages preferred the cooler autumn months. Nor did the moist conditions at Hennops River suit *O. radiatum*, as infestation virtually disappeared in tracer calves after a quite promising start (Table 13).

Near Boekenhout the first infestations of *O. columbianum* were encountered in young impala culled during the first eight days of September 1975 (Table 19), the previous months being cool with a total of only 20,8 mm of rain having fallen from May to August (Table 20), thus indicating that the larvae were able to develop to infectivity under these condi= tions.

At Queensland in Australia Durie (1962) found that mid-summer tempera= tures were unfavourable for the development of the free-living stages of *O. radiatum*, which thrived under the more moderate temperatures of spring and early summer.

Near Boekenhout (Survey 7), *O. radiatum* clearly preferred the cooler dryer months of winter and spring. This seasonal preference is even more dramatic if one considers that until May 1976 90 untreated animals had been present to seed the pastures with infestation and that only eight such animals were present from May to January 1977. It is, however, also important to consider the role of the cattle dungpat in the survival of infestation on pasture (Reinecke, 1960a, b). Thus extrapolating from Reinecke's (1960b) findings it is possible that infestation acquired during one month could result from eggs deposited one to three months previously. Consequently the large burdens of *O. radiatum* in the calves slaughtered during January 1977 could have resulted from larvae that had been freed from dungpats by the good rains of November 1976 (Fig. 8).

In the light of the preceding observations I suggest that the free-living stages of *O. columbianum* and *O. radiatum* prefer cool conditions with a mean temperature probably not exceeding 15°C. They can survive when rainfall is less than 10 mm a month, and appear to be adversely affected by continuous high rainfall or irrigation.

The parasitic life cycles of the immature stages of *O. columbianum* and *O. radiatum* are longer than those of most common nematode parasites of sheep or cattle. The first fourth stage larvae moult to fifth stage worms 21 days after infestation for the former and 19 days for the latter helminth (Reinecke, 1973; Andrews & Maldonado, 1941). Consequently no reliable observations on arrested larval development could be made in the tracer lambs and cattle slaughtered in Surveys 3, 4 and 7, as the majority of worms would in any event still be larvae because of the short period of exposure before necropsy.

The findings of Rossiter (1964) and Viljoen (1964), although pertaining to continuously exposed sheep, appear to indicate that in *O. columbianum* an arrest in development in the fourth larval stage does occur, and that this takes place from January to June or even September. If this is indeed so it agrees in part with my suggestion that the period January to March is too hot and moist for optimal survival of the free-living stages; hence the parasite bridges this period by arresting its development in the host until external conditions are more favourable. It does not explain, however, why the period of arrested development apparently extended to June or September when conditions on pasture should have been favourable for larval development and survival.

## *ARRESTED DEVELOPMENT*

Parasitic nematodes in their normal definitive hosts do not always reach adulthood within a developmental period of characteristic length, and prolonged interruption of the life cycle is a frequent alternative (Schad, 1977). This interruption is known as arrested development and has been defined by Michel (1974) as the temporary cessation of development of nematodes at a precise point in early parasitic develop= ment, where such an interruption contains a facultative element, occurring only in certain hosts, in certain circumstances or at certain times of the year, and often affecting only a proportion of the worms.

In insects a similar interruption is known as diapause and in certain species it is not facultative but obligatory (Chapman, 1972). Obligatory arrest may well occur also in nematodes at the extreme range of their distribution, where the external environment may barely permit the continued existence of the parasite (Schad, 1977).

Gordon (1973) has suggested that the term hypobiosis includes the terms arrested, retarded, inhibited or suppressed when applied to worms which have not completed their prepatent period within the commonly accepted time. Although arrested or inhibited worms are hypobiotic, the word itself does not embody the dynamism of the term "*arrested*", which implies the ability to resume development, but rather the direct opposite. Consequently the word "*arrested*" will be used in this dis= cussion although "*hypobiotic*" or "*inhibited*" may on occasion be used synonymously.

Although arrested development in nematodes generally occurs at the precise time that the larvae of ruminant parasites are in the early fourth stage of larval development, this is not always so and does not necessarily apply to nematodes of other host species. Michel (1952) found that the larvae of *Trichostrongylus retortaeformis*, a parasite of rabbits, became inhibited in the third larval stage. Similar observations have been made for *T. axei*, *T. vitrinus* and *T. colubriformis* in ewes by Eysker (1978), but I have reservations concerning this finding because the sieves he used for worm recovery had apertures of 63 µm which are too large to retain all third stage larvae. This contrasts with the observations of Southcott *et al.* (1976), who found that *T. axei* became arrested in the early fourth larval stage. *Trichostrongylus colubriformis* and other intestinal *Trichostrongylus* spp. of sheep are apparently retarded as immature adults (Muller, 1968), while *Dictyocaulus viviparus,* the lungworm of cattle is retarded as late fourth stage larvae and early fifth stage worms (Gupta & Gibbs, 1975). The other common nematode parasites of sheep and cattle, namely *Haemonchus contortus, H. placei, Ostertagia circumcincta, O. ostertagi, Cooperia oncophora, C. pectinata* and *Nematodirus* spp. all become arrested in the early fourth stage of larval development (Muller, 1968; Connan, 1971; Brunsdon, 1972; Smith, 1974; Southcott *et al.*, 1976; the present surveys). In white-tailed deer *Ostertagia* spp. are arrested as early fourth stage larvae (Baker & Anderson, 1975) as are a number of the nematodes recovered from impala in Survey 8.

Not only are there differences between species as to the stage of development at which they become arrested, but there are also differen= ces within species as to the proneness of various strains to become arrested. McKenna (1973) demonstrated differences in the degree of inhibition and in the time after storage of infective larvae that inhibition occurred, when two morphologically and geographically distinct strains of *Haemonchus contortus* were used to infest sheep. Michel *et al.* (1973) have shown that selection of strains prone to arrested develop= ment or free from it can be rapid so that strains of a particular para= site within a given locality may vary depending upon husbandry practices and micro-climate.

Numerous factors have been suggested as reasons for the occurrence of arrested development. Schad (1977) has grouped these factors into three major categories which he has listed as:-

1) External environmental factors acting on the free-living stages, which subsequently enter a diapause-like state within the host.
2) Host factors which determine the host's suitability for further development and which, when adverse, may lead to arrest.
3) Parasite-related factors which are either genetic or density-dependent.

Factors from each of the groups can act singly or together with other factors from the same or other groups to induce arrest or increase the proportion of arrested larvae over that which would occur if the stimuli acted independently (Schad, 1977).

The external environmental factors acting on the free-living stages may be chilling (Hutchinson, Lee & Fernando, 1972; Blitz & Gibbs 1972a; McKenna, 1973; Armour & Bruce, 1974; Michel, Lancaster & Hong 1975a), reduction in photoperiod (Gibbs, 1973) or ageing of the larvae (Stockdale, Fernando & Lee, 1970; Reid & Armour, 1972; McKenna 1973), and may require that the particular strain of nematode is innately susceptible to inhibition (Armour, 1970; Armour, Jennings & Urquhart, 1969). It is also possible that helminths may become adapted to a particular environment and that an arrest in development is obligatory (Waller & Thomas, 1975).

Host factors that have been suggested as possible causes of arrested development are acquired resistance (Donald, *et al.*, 1964; Dineen, Donald, Wagner & Offner, 1965), increasing age of the host (Waller & Thomas, 1975; Connan, 1975), the host's diet (Rohrbacher, 1960; Poeschel & Todd, 1969), endocrine changes in the host (Connan, 1968) and environmental factors acting on the host (Anderson *et al.*, 1965; James & Johnstone, 1967; Mitchel *et al.*, 1970b).

Parasite-related factors which could lead to arrested development are the presence of adult worms (Dunsmore, 1963; Michel, 1963) or the number of larvae dosed (Dunsmore, 1960; Donald *et al.*, 1964; Hutchinson *et al.*, 1972; Michel, Lancaster & Hong, 1975b).

In my opinion the three major categories of factors which give rise to arrested development between them result in two types of inhibition, namely non-specific and seasonal arrested development. Non-specific arrested development may be present at any time of the year and its causes are either host-related or parasite-related factors, both of which affect the immediate environment of the nematode and inhibit its development. Seasonal arrested development occurs annually during the same season. It is generally dependent upon the nematodes affected being adapted to a particular environment and susceptible to one or several seasonal external environmental stimuli acting upon the infective larvae, and resulting in arrest in a later stage of development.

Non-specific arrested development is similar to quiescence in insects which is a state of delayed development directly referable to immediate environmental conditions. If these conditions are altered, by for instance removal of adult worms or breaking down the host's resistance with immuno-suppressant compounds, the arrested larvae can immediately resume development.

Seasonal arrested development can be compared with diapause in insects in which development is inhibited in response to environmental signals which prelude the coming of adverse conditions (Chapman, 1972). Development cannot be resumed in diapausing insects, even in the presence of apparently favourable conditions, unless diapause is broken by an appropriate environmental change (Richards & Davies, 1970) or until a fixed period of diapause development has been completed (Lees, 1956). Similarly a resumption of development cannot be initiated in seasonally arrested nematode larvae by altering host or parasite-related factors, and development will resume only after a fixed period of time has elapsed. It is probable that at certain times of the year most hosts simultaneously harbour non-specifically and seasonally arrested worms, but whereas the non-specifically arrested parasites can resume development at any time, provided host- or parasite-related factors alter, the seasonally arrested parasites will resume development only after a fixed period of time has elapsed. This resumed development may not necessarily be synchronous for all larvae present.

In the present surveys seasonal arrested development of nematodes was evident in all ruminant host species and I intend discussing this phenomenon and its similarities to diapause in insects, using quotations from Chapman (1972) for comparative purposes.

"Diapause is usually restricted to one stage of the life history, but commonly an earlier stage is the recipient of the environmental signals initiating the delay in development." (Chapman, 1972). In a large number of parasitic nematodes it is third stage infective larvae that are the recipients of environmental signals and early fourth stage larvae which are arrested in their development (Hutchinson *et al.*, 1972; Blitz & Gibbs, 1972a; McKenna, 1973; Armour & Bruce, 1974).

"Sometimes every individual in every generation enters diapause. This is obligatory diapause and as a result there is usually only one generation each year. Alternatively, in other species, some generations may be completely free of diapause while in others some or all may enter diapause. This is facultative diapause and as a rule there are two or more generations per year." (Chapman, 1972). The seasonal fluctuations of *Ostertagia ostertagi* in cattle in Scotland (Anderson *et al.*, 1965) and *Haemonchus contortus* in sheep at Armidale in Australia (Southcott *et al.*, 1976) and on the Transvaal Highveld (Surveys 3 to 5), indicate that there are two or more generations of each of these nematodes annually. The generation or generations acquired in spring or early summer are relatively free from larval inhibition while in infestations acquired during autumn some or all larvae may become arrested.

Obligatory arrested development may be essential for the survival of nematodes at the extreme range of their geographic distribution, as external environmental conditions may for most of the year be unfavour= able for the development or survival of their free-living stages. This is probably why a single generation only of *Haemonchus contortus* occurs annually in north-east England, the major portion of the year being spent in the host as arrested fourth stage larvae (Waller & Thomas, 1975).

"Although facultative diapause is largely controlled by environmental factors, different races of a species may become genetically differen= tiated with respect to diapause....... and each of these responds differently to environmental factors." (Chapman, 1972). An analogous situation exists in a number of nematode species. In Scotland environ= mental influences acting on infective larvae of *Ostertagia ostertagi* during autumn result in arrested development of fourth stage larvae in cattle during late autumn and winter (Armour & Bruce, 1974), while in parts of Australia it is larvae of this species ingested in spring that may be arrested in their development (Hotson, 1967). *Ostertagia* spp. infestations acquired by sheep either in England or on the Transvaal Highveld during winter exhibit a high degree of larval arrest (Connan, 1971, Surveys 3 to 5), while at Armidale in Australia it is infesta= tion acquired during spring that exhibits this tendency (Southcott *et al.*, 1976). In semi-arid areas desiccation may be the stimulus for subsequent arrest of worms of this genus in sheep (Shimshony, 1973, cited by Armour & Bruce, 1974). *Haemonchus contortus* ingested by sheep during summer in north-east England (Waller & Thomas, 1975), as opposed to autumn in the south of England (Connan, 1971), New South Wales (Southcott *et al.*, 1976) and the Transvaal Highveld (Surveys 3 to 5) were subject to larval arrest. Thus parasites of the same genus or species seemingly responded differently to different stimuli at different localities.

"The most reliable and consistent indicator of seasons is day length or photoperiod and this is the most important of the sign stimuli initia= ting diapause. Other possible indicators are temperature, the state of the food, and the age of the parent." (Chapman, 1972). In nematodes chilling is probably the most important of the sign stimuli (Hutchinson *et al.*, 1972; Blitz & Gibbs, 1972a; McKenna, 1973; Armour & Bruce, 1974), although it has been shown by Gibbs (1973) that photoperiod does have an effect. Smith (1978), however, has demonstrated that daily photoperiods of eight or 16h during storage of infective larvae had no effect on the subsequent degree of inhibition exhibited by *Cooperia oncophora* in calves. He also found that temperature con= ditioning the eggs of this species did not result in arrested develop= ment of the worms subsequently cultured from these eggs, but that it was infective larvae that were sensitive to temperature condition= ing.

It can be assumed that species with extensive geographical distribu= tions are differently adapted to temperature or photoperiod in different parts of their ranges and that these differences become inherited characteristics of the populations. Thus, the third stage infective larvae of *Ostertagia* spp. and *Haemonchus contortus* in their various habitats respond at different seasons of the year to seasonal environmental stimuli. However, the mean midsummer temperature in north-east England (Waller & Thomas, 1975) is similar to the mean autumn temperature in the south of England (Gibson & Everett, 1976) and the mean early winter temperature at Armidale in New South Wales (Southcott *et al.*, 1976) and at Hennops River (Surveys 3 and 4). It would thus appear that if temperature is the stimulus for *H. contortus* to become arrested in its development the same mean temperature is effective, albeit in different seasons in these widely dispersed localities.

In insects a number of photoperiodic cycles are necessary to produce an effect (Chapman, 1972). Similarly in nematodes, in which temperature appears to play a more important role than photoperiod, the length of time infective larvae are exposed to cold is important (Stockdale *et al.*, 1970; Hutchinson *et al.*, 1972; Armour & Bruce, 1974; Michel, Lancaster & Hong, 1974). The longer the larvae are stored at a low temperature the higher the subsequent degree of inhibition; if, however, a certain optimal time of storage is exceeded the process is reversed (Michel *et al.*, 1974).

It is thus evident that there are considerable areas of similarity between arrested development in nematodes and diapause in insects. Even greater similarities become apparent if the seasonal occurrence of arrested development in *H. contortus*, which has an extensive geographical distribution, is compared with that of diapause in the parasitic first instar larvae of *Oestrus ovis*, the equally extensively distributed nasal bot fly of sheep.

In the cold climates of Canada and New Zealand, where survival outside the host is impossible for much of the year, *O. ovis* survives during autumn and winter as first instar larvae in the nasal passages of sheep, maturing to second and third instar larvae in spring and then developing to pupae and adults on pasture during summer (Fallis 1940; Kettle, 1973). This prolonged period of diapause permits the development of only one or two generations a year, as is probably the case with *Haemonchus contortus* in north-east England (Waller & Thomas, 1975) and the south of England (Connan, 1971). In the warmer climates of Texas, Kentucky and the Transvaal Highveld diapause is present only in some of those larvae of *Oestrus ovis* deposited in late autumn and winter and these larvae resume development in early spring (Cobbett & Mitchell, 1941; Rogers & Knapp, 1973; Horak, 1977); other larvae complete their parasitic life cycles in approximately 30 days and numerous generations are possible annually. This type of life cycle corresponds to that of *Haemonchus contortus* in New South Wales (Southcott *et al.*, 1976) and on the Transvaal Highveld (Surveys 3 to 5).

That this period of arrested development in *Oestrus ovis* is indeed diapause and not just quiescence brought about by cold winter temperatures is proven by the fact that the temperature in the nasal passages may be constant irrespective of the external temperature (Rogers, Knapp, Cook & Crow, 1968). Thus arrested development in the first instar of *O. ovis* is true diapause as it has not been caused by the effect of the immediate environment on the larvae but rather by a stimulus received during an earlier stage of development, namely the parent larviparous fly. Similarly the abomasal temperature at which *Haemonchus contortus* find themselves is constant and does not contribute to their state of arrested development.

The morphological and biological characteristics of arrested larvae have received but scant attention. Many authors describe the larvae as early fourth stage larvae but go no further. Blitz & Gibbs (1971b), however, described the morphological characteristics of arrested larvae of *H. contortus* in sheep. They found that these larvae were arrested at a precise stage corresponding in the males to the early fourth stage of development, normally attained three to four days post-infestation (Veglia, 1915) with no apparent differentiation of the genital primordium. The females were arrested at a slightly later stage and some sexual differentiation was evident. The length of both male and female larvae was 1 215 µm $\pm$ 138,5. Conspicuous crystals were present in the intestinal cells of these larvae, but disappeared as the larvae recommenced development. Bird, Waller, Dash & Major (1978) examined and analysed crystals which they found in the intestinal cells of inhibited *H. contortus* larvae. They thought that these crystals are not characteristic of arrested larvae but are rather the by-products of degenerative processes in both developing and arrested larvae.

Although the larvae are arrested in their development they do not appear to be entirely non-pathogenic. Armour & Bruce (1974) found that the plasma pepsinogen levels of calves infested with arrested *Ostertagia ostertagi* were slightly higher than the levels recorded before infestation, and Sinclair & Prichard (1975) concluded that arrested larvae of *Haemonchus contortus* in sheep may cause damage to the abomasal mucosa resulting in elevated plasma pepsinogen and abomasal pH levels and somewhat greater abomasal leakage of plasma constituents.

Moreover the larval burdens are not necessarily static. McKenna (1974a) found that the bulk of arrested *H. contortus* larvae were lost within 10 weeks of artificial infestation before they attained sexual maturity, and Waller & Thomas (1975) concluded that, in lambs continuously exposed to infestation with larvae of *H. contortus* which were prone to inhibition, the parasitic phase of the life cycle lasted four weeks before elimination occurred. Brunsdon (1972), however, considered that heavy infestations with arrested fourth stage larvae of *Ostertagia* spp. in calves resulted from a process of slow accumulation over the grazing season, and Armour & Bruce (1974) found that there was virtually no reduction in the burden of arrested larvae of *O. ostertagi* in artificially infested calves for a period of 16 weeks, and thereafter maturation of these larvae took place.

The differences in rates of elimination between *Haemonchus* spp. and *Ostertagia* spp. could largely be due to the sites occupied by their larvae in the abomasum. A larger proportion of *Haemonchus* spp. larvae than of either *Ostertagia* spp. or *Longistrongylus* spp. (an *Ostertagia*-like nematode) larvae was recovered from the abomasal ingesta in the present surveys, while the converse was true for the mucosal digests. These findings confirm those made for *Haemonchus contortus* by Blitz & Gibbs (1971b) who stated that arrested develop= ment of this parasite is not associated with the histotropic phase of the life cycle. Thus a greater proportion of *Haemonchus* spp. larvae is likely to be exposed to ingestal flow and consequently mechanical removal because they are free in the ingesta or only loosely attached to the mucosa than of *Ostertagia* spp. or *Longistrongylus* spp. larvae which are largely present in the lumina of the gastric glands.

Southcott *et al.* (1976) have suggested that inhibited development should be considered in relation to the probable fate of current egg deposition, and that larvae become inhibited at a time when eggs currently being deposited have little chance of giving rise to appreciable levels of pasture infestation. Thus at a particular locality with a temperate climate the degree and duration of arrested development of the various nematode species will depend on the probable fate of currently deposited eggs. This observation can be substantia= ted by comparing concurrent infestations of *Haemonchus contortus* and

*Ostertagia* spp. in sheep. The former does not survive well on pasture during winter (Gibson & Everett, 1976; Southcott *et al.*, 1976) while the latter does (Gibson & Everett, 1972; Southcott *et al.*, 1976), and the degree of arrested development of *Haemonchus contortus* and its duration during winter invariably exceeds that of concurrent *Ostertagia* spp. infestations (Viljoen, 1964; Muller, 1968; Connan, 1971; Southcott *et al.*, 1976; Surveys 3 to 5).

The geographic distribution of *Haemonchus placei* and *Ostertagia ostertagi* of cattle does not appear to overlap, because no surveys have been conducted in areas where overlapping does occur, and thus no comparisons can be drawn on the degree of duration of arrested development in concurrent infestations with these two nematodes. In Surveys 6 and 7 *Haemonchus placei* and *Cooperia* spp. were present in the survey cattle and both the degree of arrested development and its duration were greater in the former than the latter species. This difference can be explained by the greater resistance to heat, cold and desiccation of the free-living stages of *Cooperia* spp. than those of *Haemonchus placei* (Reinecke, 1960b).

The results of Survey 8 (impala near Boekenhout) are particularly interesting in the light of the foregoing discussion in that five genera were arrested in their development. The degree and duration of arrested development were similar for *H. placei*, *Longistrongylus sabie* and *Impalaia tuberculata* but considerably less and shorter for the *Cooperia/Cooperioides* group. Winter near Boekenhout is dry, fairly warm and with little cloud cover, and arrested development of the former three species during winter is probably a reflection of the inability of their free-living stages to survive these conditions. The free-living stages of *Cooperia* spp., however, are resistant to adverse conditions (Reinecke, 1960b) and hence the pressure for their development to be arrested would be less severe.

Differences in arrested development between *Ostertagia* spp. and *Trichostrongylus axei*, both abomasal parasites, on the one hand and intestinal *Trichostrongylus* spp. on the other deserve further discussion. The studies in England of Gibson & Everett (1967, 1972) and Boag & Thomas (1970) with *Ostertagia circumcincta* and *Trichostrongylus colubriformis* and in Australia with *Ostertagia* spp. (mainly *O. circumcincta*), *Trichostrongylus axei* and intestinal *Trichostrongylus* spp. (mainly *T. colubriformis)* by Southcott *et al.* (1976) indicate that their survival on pasture is fairly similar. Yet *Ostertagia* spp. and *Trichostrongylus axei* became arrested in the fourth larval stage while intestinal *Trichostrongylus* spp. did not exhibit this phenomenon.

Muller (1968) has suggested that intestinal *Trichostrongylus* spp. become arrested as adolescent fifth stage worms during times of adverse climatic conditions. The sieves he used for worm recovery, however, had apertures of 150 μm and these would not have retained third or fourth stage *Trichostrongylus* spp. larvae had they been present. Blitz & Gibbs (1972b), however, felt that the worms described by Muller (1968) were stunted adults rather than arrested adolescents and a detailed study is necessary to determine whether intestinal *Trichostrongylus* spp. do exhibit arrested development or not and in what stage of development this occurs.

During diapause in insects morphogenesis ceases but a gradual process of physiological development takes place before growth can be resumed. Andrewartha (1952), cited by Lees (1956), describes this process as diapause development. The duration of this period can vary considerably with temperature and photoperiod and from species to species, but under optimum conditions it is fairly constant within a particular species (Lees, 1956; Chapman, 1972) and may also cease spontaneously after a fixed period of time (Beck, 1968,cited by Armour & Bruce, 1974).

Morphogenesis ceases early in the fourth larval stage in many of the common parasitic nematodes exhibiting seasonal arrested development (Anderson *et al.*, 1965; Blitz & Gibbs, 1971b; McKenna, 1973). It is quite probable that a period of diapause development is a prerequi= site to further morphogenesis in these larvae, and as the temperature in the gastro-intestinal tract of the host animal is constant it can be assumed that the length of this period will also be reasonably constant for a particular species.

Armour & Bruce (1974) artificially infested calves with infective larvae of *Ostertagia ostertagi* which had previously been chilled at $4^{o}C$ for five weeks in order to produce a large proportion of arrested larvae. After anthelmintic removal of the adult worms that might have developed they found that larvae spontaneously resumed development

16 to 18 weeks after infestation.

In an even more striking demonstration of the fixed period of seasonal arrested development, Blitz & Gibbs (1971a) surgically transferred arrested larvae of *Haemonchus contortus* from naturally infested ewes to parasite-free ewes maintained under worm-free conditions. Ten to 12 weeks after this transfer the worms matured causing a marked rise in faecal worm egg count which coincided with a marked mid-April rise observed in the egg counts of sheep in other experiments.

If the duration of seasonal arrested development is predetermined then larvae acquired in early autumn should mature sooner than those acquired later, yet the time of maturation within a species appears to be reasonably synchronised. The period during which maturation occurs may be fairly short in infestations with *H. contortus* and longer in those with *Ostertagia* spp. (Michel, 1974). There are a number of actual and possible factors that could bring about this synchronisation.

In many regions and with many species the greatest availability and ingestion of infective larvae occur over a relatively short period and this may coincide with the time that inhibited development of these larvae is at its height (Connan, 1971; Southcott *et al.*, 1976; Surveys 3 to 7). Thus if the period of arrested development is constant the greatest proportion of seasonally arrested larvae of a particular species can be expected to mature at approximately the same time.

It has been demonstrated that if larvae which have been conditioned to become arrested are not ingested, the changes that have taken place are reversible and with the passage of time these larvae, if ingested, will not become arrested (Armour & Bruce, 1974; Michel *et al.*, 1974). This seems to indicate that once larvae are conditioned, the physiolo= gical processes that have to be completed before they can resume development commence irrespective of whether they are ingested or not. Armour & Bruce (1974) found that conditioned larvae of *O. ostertagi* stored for eight weeks resulted in maximum inhibition but that this declined markedly between eight and 19 weeks of storage. Michel *et al.*

(1974) recorded maximum inhibition in calves when infested with larvae of *O. ostertagi* stored at 10$^{o}$C for 12 weeks and a marked decline in inhibition if larvae from the same batch were used but stored for longer beforehand.

It is thus possible that both inside the host and in conditioned free-living stages, changes associated with arrested development are reversed within the same period and although conditioned larvae are ingested at various times their development to adulthood will be reasonably synchronised.

Michel, Lancaster & Hong (1976) exposed yearling cattle in the south of England during autumn to grazing infested with *O. ostertagi*. These animals were housed at the end of December under conditions designed to preclude further infestation and their worm burdens studied after slaughter at intervals until summer. They concluded that a small constant number of arrested larvae resumed development every day but that this rate was markedly increased during March so that nearly all arrested larvae had developed by the beginning of April, thus indicating synchronisation in the development of the majority of arrested larvae.

Once diapause development is complete morhogenesis is resumed provided environmental conditions are suitable. If they are not the insect remains in a state of quiescence until they become more favourable (Chapman, 1972). If diapause in insects and seasonal arrested development in certain nematodes is analogous the completion of the period of seasonal arrested development in the host does not necessari=ly mean that morphogenesis will resume. Host- or parasite-related inhibiting factors may now come into play and the larvae may enter a state of non-specific arrested development, and may resume development once their immediate environment alters. This resumed development may be either gradual or sudden, depending upon the inhibiting factors and the manner of their removal.

One could conclude that the observations of Michel *et al.* (1976) con=tradict the above hypotheses. They stated that large numbers of arrested larvae of *O. ostertagi* could develop to adulthood at a time earlier than usual because of a breakdown in host resistance. If, however, one examines the worm burdens of the calves in their experiments it is obvious that the south of England is a reasonably favourable region for *O. ostertagi*, as fairly large numbers of adult worms and developing fourth stage larvae were present even in the middle of winter and thus only some larvae were seasonally arrested. One can also assume that, because of the very large worm burdens present in the calves, host- and parasite-related factors would also come into play causing inhibition of development of other larvae. With the breakdown of host resistance, those larvae retarded because of host-related factors resumed development and caused disease, while the seasonally arrested larvae remained so, as can be seen from the large residual burdens of early fourth stage larvae in the diseased animals. Thus rather than contradicting my hypothesis the findings of Michel *et al.*(1976) confirm the multitude of factors that may give rise to larval inhibition and show that arrested larvae may react differently to the removal of these inhibiting factors.

The maturation of seasonally arrested larvae, usually during spring, has given rise to the phenomenon known as spring rise in faecal worm egg counts (Michel, 1974). It is this increase in egg output which is responsible for contamination of pastures at the commencement of a season generally favourable for the development and survival of the free-living stages. In those nematode species in which the degree of pasture contamination or conditions at pasture during winter do not allow for survival of any larvae, or in host animals that are housed during winter, the spring rise in egg out put will be due solely to resumed development of arrested larvae (Procter & Gibbs, 1968a, b; Boag & Thomas, 1971). In other species, which survive the winter on pasture, albeit in small numbers, the spring rise will be due to resumed development of arrested larvae and rapid maturation of newly ingested infestation (Thomas & Boag, 1972).

The short duration of the spring rise in lambs, male and non-parturient female sheep may be caused by the developing parasites triggering a self-cure-like reaction in the host, resulting in the expulsion of most of the worm burden (Blitz & Gibbs, 1972b).

In pregnant or parturient ewes the spring rise may coincide with parturition, in which event high faecal worm egg counts may be present for a considerable time. This phenomenon has been termed the peri-parturient rise in egg counts by Salisbury & Arundel (1970), and is associated with lactation (Procter & Gibbs, 1968a, b; O'Sullivan & Donald, 1970). It is due to the immune expulsion of gastro-intestinal nematodes being impaired during lactation by inhibition of the lymphocyte-mediated component of the immune reaction. This impair= ment of expulsion is probably primarily of endocrinal origin, and prolactin and the adrenal glucocorticoids possibly play an inter= related role (Connan, 1976).

Adult worms that have developed from arrested larvae persist in these ewes (Blitz & Gibbs, 1972b), fecundity of female worms increases (Connan, 1976) and there is an increased rate of establishment of new= ly acquired infestation (O'Sullivan & Donald, 1970). Thus the peri-parturient rise in egg counts results in prolonged pasture contamina= tion precisely during that time when new-born susceptible hosts are available.

In conclusion it is my opinion that seasonal arrested development in nematodes is similar to diapause in insects. It is trigged by stimuli of which temperature and to a lesser extent photophase are probably the most important, acting on the free-living stages and resulting in inhibited development in a subsequent stage of the life cycle. Non-specific arrested development occasioned by host- or parasite-related factors is similar to quiescence in insects, in that the immediate environment exercises a restraining influence.

## *CONTROL MEASURES*

Although these surveys were conducted primarily to ascertain the epizootiology of helminth infestation in certain domestic and wild ruminants in the Transvaal, an important consideration is the applica= tion of the knowledge so obtained to the control of helminth infesta= tion. Despite husbandry playing an important part in any control programme it is in the development of highly effective anthelmintics and their application that the greatest strides have been made, and I will concentrate on this aspect of control.

The eight possible uses of anthelmintics have been listed by Gordon

(1973) and Kelly, Gordon & Whitlock (1976). These uses are (1) curative to deal with clinically apparent disease (2) tactical when an emergency is recognised (3) strategic based on the epizootiological pattern of infestation (4) diagnostic in the differential diagnosis of ill-thrift (5) experimental to manipulate the experience of infestation (6) immunologic to assist the acquisition of resistance (7) special to take advantage of particular attributes of an anthelmintic (8) extended aimed at giving an extended effect because of the epizootiology of infesta= tion at the time of treatment. Of these I suggest four for the routine control of nematode infestation in animals in those regions of the Transvaal in which frost occurs or may occur during winter. These four are:-

1) Tactical or expeditious use - based on epidemiological con= ditions such as climate, grazing or management that will be conductive to an outbreak of helminthosis, i.e. treat when worm burdens are at their height.

2) Strategic or epidemiological use - based on a thorough knowledge of the seasonal incidence of infestation, the occurrence of arrested development, regular husbandry practices and life cycle patterns such as times of parturition and weaning, i.e. treat before worm burdens reach a peak.

3) Special or exceptional use - this use takes advantage of unique attributes of an anthelmintic such as the ability to control infestation by daily low level administration or by the pro= longed effect of a single dose or injection.

4) Extended use - a single administration is aimed at giving an extended effect such as removing worms at a time when reinfesta= tion from pasture is minimal, or before placing animals on newly-established clean pasture, or at cleaning out pregnant animals to reduce the source of infestation they pose for their offspring.

Treatment of the various ruminant groups will be discussed separately, but it is first necessary to discuss the control of arrested larvae.

*Arrested larvae*

Arrested larvae of the commonly encountered sheep nematodes are less susceptible to anthelmintics than are normally developing larvae (Horak *et al.*, 1972; Snijders, Horak & Louw, 1973; McKenna, 1974b), but increasing the dosage of the anthelmintic improves efficacy (Armour, Bairden & Reid, 1975). In cattle, however, even high dosage rates may fail to remove arrested *Ostertagia ostertagi* (Reid, Armour, Jennings & Urquhart, 1968; Craig & Bell, 1978) and repeated treatments may be necessary (Gordon, 1973).

One of the reasons for arrested development is that the external environment is unfavourable for development or survival of parasites. Hence elimination of arrested larvae will extend the effect of the anthelmintic as little new infestation will be acquired. In addition it will also reduce future contamination of the pasture as there should be fewer or no larvae developing to adulthood at the termina= tion of the period of arrested development.

*Sheep*

All animals should be treated during July with a broad-spectrum anthelmintic effective against arrested larvae. This treatment will control arrested fourth stage larvae of *Haemonchus contortus*, adult and arrested *Ostertagia* spp., adult *Trichostrongylus* spp. and *Oesophagostomum columbianum* acquired during April and May. It will also have an extended effect, for with the possible exception of *Ostertagia* spp., little reinfestation will take place before November or December.

A strategic drench, utilizing a broad-spectrum anthelmintic with a special effect in that it must also control cestodes, should be administered during November. This will control *Ostertagia* spp., *Moniezia expansa* and the small number of nematodes acquired during the preceding months.

From January to April broad- and narrow-spectrum anthelmintics effective against *Haemonchus contortus* can be administered alternate= ly. The intervals between dosing will depend on the intensity of infestation and on the occurrence of warm wet weather, and will vary between four and eight weeks. This amounts to alternation between tactical and strategic drenching and is aimed at *H. contortus*, but will also control other nematodes. A broad-spectrum anthelmintic with a cestocidal effect should be incorpora= ted into this programme during February or March for the strategic control of nematodes and *Moniezia expansa*.

As an alternative measure disophenol can be administered during January and by virtue of its prolonged chemoprophylactic effect should control *Haemonchus contortus* for the following two or three months (Reinecke, 1977). Provided faecal worm egg counts are moni= tored during this period any increase in infestation due to other species can be controlled with a broad-spectrum anthelmintic.

Reinecke (1964) has recommended the offensive use of anthelmintcs, which implies drenching when a helminth species is already at a low level in its host, and suggested that treatment to control *H. contortus* in the Karoo and Border areas of the Cape Province should be administered during September. Thomas (1967) proposed that on the Transvaal Highveld this treatment be brought forward to May.

In the light of the present findings May would be too early at certain localities as reinfestation could take place thereafter, and September unnecessarily late as little infestation is acquired after July.

Employing a drenching programme reasonably similar to that suggested, but incorporating strategic treatments for the control of the larvae of the nasal bot fly *Oestrus ovis*, Horak *et al.* (1976) were able to demonstrate a significant difference in live mass gains and a difference in mean fleece masses of treated and untreated lambs running with the lambs in Survey 5, and this despite the apparently low level of infestation.

*Cattle*

A broad-spectrum anthelmintic should be administered during July and provided it is effective against arrested larvae, it will have an extended effect against *Haemonchus placei*, *Cooperia* spp. and *Trichostrongylus* spp. and act as a strategic drench against *Oesophagostomum radiatum*. A broad-spectrum anthelmintic administered strategically during December will control immature and adult forms of the same parasites, and during March will control *Haemonchus placei* and *Cooperia* spp. If infestation with adult *Haemonchus placei* is particularly severe from January to May, treatments with narrow-spectrum anthelmintics effective against this species can be alternated with the latter treatments during this time.

### *Antelope*

The large-scale treatment of free-ranging antelope is virtually impossible. If, however, these animals have to be captured for any purpose treatment can be administered then. This can be done orally if the animals are not sedated but must be administered by injection if they are, because of difficulty that may be experienced with deglutition.

Treatment is particularly important if animals are captured for trans= location. Not only does this eliminate the extra stress of a heavy worm burden at the new locality, but it also prevents the introduction of helminth species not already present in a particular area. If the springbok introduced into the Bontebok Park at Swellendam had been treated for lung worm prior to their release, deaths which subsequent= ly occurred in bontebok due to *Dictyocaulus magnus* infestation (Verster, 1973 cited by Heinichen, 1973), could possibly have been prevented.

If antelope are confined on farms or in small game parks, anthelmintics can be administered by means of feed blocks or licks. Anthelmintics capable of controlling arrested larvae should be used and the ideal time to administer medication in this form is during July. Not only will antelope consume blocks or licks more readily because of the paucity of grazing, but treatment will have an extended effect on certain species until approximately October.

# SUMMARY

The seasonal fluctuations in the worm burdens of pigs, sheep, cattle, impala and blesbok exposed to infestation on improved or natural pastures in the Transvaal were determined. The prevalence of infestation in pigs slaughtered at the Pretoria Municipal Abattoir and in impala near Pafuri and blesbok at Badplaas was also established.

Sheep, goats and cattle were successfully artificially infested with a number of nematodes of impala origin and sheep with those of blesbok origin.

The various methods used to determine the seasonal incidence of helminth parasites are discussed and the wastage of valuable material criticised when complete recoveries of both internal and external parasites are not attempted at each necropsy.

Host specificity and the distribution of parasites according to climate and the zoogeographical distribution of their hosts are discussed and the epizootiology of the major nematode genera parasitizing sheep, cattle, impala and blesbok in the Transvaal is determined.

The phenomenon of arrested development in nematodes is compared with that of diapause in insects and measures to control helminth parasites in domestic stock and antelope in the Transvaal are suggested.

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