Helminth infections: Domestic ruminants: Introduction

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INTRODUCTION

Helminthology is the study of worms, be they roundworms, flatworms, parasitic or free-living. Many scientists have contributed to the science of helminthology, and currently approximately 5 000 articles on animal parasites are published annually. These deal with all aspects of helminthology, such as taxonomy, morphology, clinical pathology, immunology, pathogenesis and pathology, and epidemiology.

While the parasitic worms, or even the thought of them, may seem revolting, we should never forget the old adage, 'unknown is unloved'. The helminth parasites have a beauty of their own, and are so well adapted to their natural hosts, that they have intricate and highly complex life cycles to enable them to survive, and all these aspects make them extremely interesting to study. Also taking into account that very many species are still unknown to science, it is a challenging field in which much remains to be done. However, a complicating factor is that the study of helminth biodiversity is an invasive process which is frowned upon by farmers, commercial and subsistence, and animal rights activists. Because many parasites are internal it is not possible to remove them and leave the host alive, and artificial media for maintaining parasitic larval and adult stages are not in common usage.

This course deals with approximately 30 worm species out of thousands that parasitise production animals, companion animals, wild mammals, birds, fish amphibians and reptiles, insects and other arthropods, and even plants.

Table: The helminths of domestic ruminants

<table>
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<th>Helminths of domestic ruminants</th>
<th>Trematodes (Flukes)</th>
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<td>Armillifer armillatus</td>
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<td>Trichinella spiralis</td>
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SOME DEFINITIONS

The **definitive host** or **final host** is the host in which the parasite attains sexual maturity and is able to reproduce.

The **intermediate host** is the host in which the immature stage of a worm develops, so as to become infective to the final host. Usually the L1, L2 and L3 occur in the intermediate host. This host is absent in the life cycles of many of the nematodes but is present in all of the trematodes and cestodes.

The **paratenic host** or **transport host** is similar to the intermediate host, but no development of the larva takes place. There may be more than one paratenic host involved in a life cycle and larvae can pass passively (e.g. by being swallowed) from one paratenic host to the next. The larvae can continue this cycle until they die or are swallowed by the final host, in which they will resume the usual life cycle. Paratenic hosts are not essential in the life cycle.

A **reservoir host** is an animal that harbours the parasite, but is not adversely affected by it. Wild ruminants do not readily show clinical signs, but may be the reservoir hosts of the parasites of domestic ruminants, which usually react severely to infections.

The **life cycle** describes the development of a parasite through its various stages, viz. fertilization, laying of eggs, hatching and development of the larvae (in nematodes usually four larval stages, in cestodes usually two), infection of the final host and further development into adults. Two types of life cycle are recognized, namely direct or monoxenous life cycles in which intermediate hosts do not play a role and indirect or heteroxenous life cycles in which one or more intermediate hosts are necessary for their completion.

The **prepatent** or **developmental period** is the time that elapses after the infective stage has entered the final host and before the parasite demonstrates its presence by, for instance, eggs in the faeces, blood or mucus in the faeces or the urine, loss of condition or other clinical signs. This period refers to the period between infection and the presence of adult worms.

The term **infective** refers to a stage in the life cycle of a parasite when it is able to enter the next host. In the case of nematodes, either the egg that contains a first stage larva or the first stage larva is infective to the intermediate host, while the third larval stage is usually infective to the final host. In the case of trematodes the miracidium is infective to the intermediate host and either the cercariae or the metacercariae to the final host. The eggs of cestodes are usually infective to the intermediate host, while the metacestode, such as a cisticercus, coenurus, hydatid or strobilocercus, is infective to the final host. The terms infect and infection refers to the process of entering either the intermediate or the final host.

**Hypobiosis** and **hypobiotic** refer to a resting stage in the life cycle that the 4th larval stages of some of the nematodes undergo in the final host before they develop into adult worms. The term includes terms such as arrested, retarded, inhibited or suspended development and is similar to diapause in insects. It is a strictly seasonal occurrence that is triggered by normal seasonal changes in climate.
Histotrophic phase or prolonged histotrophic phase is induced by the immune status of the host rather than the season. The larvae, usually the fourth stage, remain in the host's tissues without any further development. It is a normal part of the life cycle of many nematodes.

Ecology is the study of the interrelationships between organisms and their environment. Abiotic factors such as temperature, humidity, pH, the presence or absence of light and others, which are necessary for the survival of the worms, play an important role. Ecological studies usually apply to the free-living stages of the parasites.

The intensity of infection indicates the number of individuals of a particular parasite species in each infected host. This is expressed as a number, for instance, an intensity of 2 500 means that the host is infected with 2 500 parasites. The mean intensity refers to the total number of individuals of a particular parasite counted in all the animals, divided by the number of infected hosts.

The prevalence is the number of individuals of a host species infected with a certain parasite divided by the number of hosts examined and is expressed as a percentage. For example: during a survey 200 sheep were examined and 134 found to be positive for *Haemonchus contortus*. The prevalence is: 134 divided by 200, or 67 per cent.

Apart from the above definitions, there are a number of terms that are in everyday use, the meaning of which will become clear as the course develops.

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**HOST-PARASITE INTERACTIONS – DEFENCE MECHANISMS**

**Non-immunological defence mechanisms**

**Helminth factors**

Intraspecies and interspecies competition is known to occur in helminth infestations and this may have a very definite effect on the number of worms that reach maturity.

With intraspecies competitions, the presence of adult worms frequently prevents larval stages from developing further and in the case of cestodes it is hypothesized that the original dose of eggs may stimulate rejection of subsequent doses. This has subsequently been shown to occur, and the antigens released by the larvae upon hatching stimulates an immunity that rejects or inhibits subsequent infections. It forms the basis of vaccination against some *Taenia* spp. (see 'Vaccination against helminths' below). In addition, the presence of cestode larvae, e.g. that of *Taenia saginata* in calves, inhibits the development of newly acquired ones.

In interspecies competition, competition for mutual habitats and nutritional requirements serves to control the numbers and species composition of the helminth population. The 'first come, first served' principle is very much in evidence in the case of *Haemonchus contortus*,
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Teladorsagia circumcincta and Trichostrongylus axei, where the first one to arrive in the abomasum, renders the environment unsuitable for those that follow.

Host factors

Factors that affect the final helminth burden include the age and sex of the host; these appear to be largely under hormonal control. Thus, in animals whose sexual cycle is seasonal, parasites tend to synchronize their reproductive cycle with that of the host. For instance, ewes show a 'spring rise' in faecal nematode ova, especially those of H. contortus, which coincides with lambing and the onset of lactation. Similarly, the infective larvae ingested in autumn tend to be retarded until spring. The most evolved techniques of infestation, which are under hormonal control, are those of the milk-borne nematodes, where the offspring are infested by drinking milk from an infested mother e.g. Toxocara, Strongyloides and Ancylostoma.

Immunological defense mechanisms

The immune system has not been conspicuously successful in producing resistance to helminth infestations in mammals, but this is hardly surprising since most helminths are obligatory parasites that have adapted to such an existence. During the adaptation period, the parasites have learned to deal with the immune systems of their hosts. Helminths are not maladapted pathogenic organisms, but rather fully adapted obligate parasites whose existence depends on reaching some form of compromise with the host. If an organism of this type causes disease it is likely to be very mild or subclinical. Only when helminths invade a host to which they are not fully adapted or if they occur in unusually large numbers does acute disease occur.

Humoral mechanisms

In general, helminths occur either in the gastro-intestinal tract or in the tissues, usually as larvae. The immune responses to these situations are obviously different. The most significant immunoglobulin against helminth infections is IgE, although IgM and IgG also play a minor role. IgE levels are usually elevated in parasitized individuals and many helminth infections (e.g. oesophagostomosis, ancylostomosis, strongyloidosis, bilharzia and taeniosis) are associated with the characteristic type I hypersensitivity, such as eosinophilia, oedema and urticarial dermatitis. Many of the helminths that infect their hosts percutaneously elicit a passive cutaneous anaphylaxis (PCA), a direct response to the antigens they liberate.

One of the best examples of IgE production and the allergies that result from it is the 'self-cure' phenomenon, which is seen in sheep infected with especially H. contortus. Those worms that are embedded in the abomasal mucosa secrete antigens during their 3rd moult. As a result, a local type I hypersensitivity develops locally; the combination of helminth antigen and mast cell bound IgE leads to mast cell degranulation and the release of vasoactive amines. These compounds stimulate smooth muscle contraction and increase vascular permeability, resulting in violent contraction of intestinal muscles together with an influx of fluid into the intestinal lumen. This combination results in the dislodgement of the worms and the major portion of the infection is expelled. In sheep that have just undergone self-cure, the PCA antibody titre is high. However, as there are different types of self-cure, not
all the nematodes are always excreted. Classical self-cure leads to the loss of the existing infection and the establishment of a new one; self-cure and protection entails the loss of the existing infection without the establishment of a new one; hyperinfection occurs when the existing infection is not lost and the new infection is established and premunity, where the existing infection is not lost and the new one is not established.

A similar situation occurs in calves infected with *Fasciola hepatica*, where peak PCA titres coincide with the expulsion of the flukes.

In addition to mast cells, macrophages, platelets and eosinophils also possess IgE receptors. These cells can therefore also be sensitized by IgE and will bind to the parasites. Macrophages show elevated lysosomal enzymes and increased release of reactive oxygen metabolites, interleukin 1, leukotrienes, prostaglandins and platelet activating factor. Eosinophils are attracted to sites of helminth activity by ECF-A (eosinophil chemotactic factor of anaphylaxis), released by degranulating mast cells. This material mobilises the eosinophils into the circulation and it is for this reason that eosinophilia is so characteristic in helminth infections.

Once they arrive at the site of helminth invasion, eosinophils attach to the parasites by means of IgE and IgG and degranulate. The granule contents include the superoxides, hydrogen peroxide and free radicals, and potent lytic enzymes such as lysophospholipase and phospholipase D. More important, however is that the basic protein of the granules can cause direct damage to the cuticle and thus promote the adherence of additional eosinophils. The helminthicidal effects of eosinophils are enhanced by mast-cell derived factors such as histamine and complement, and by factors derived from T-lymphocytes and macrophages.
The mechanisms involved in self-cure (Redrawn after Tizard, 1982)

While IgE-mediated antihelminth response is possibly the most significant, antibodies of the other immunoglobulin classes also play a role. Migrating helminth larvae may be immobilised by antibodies through a number of mechanisms, such as antibody-mediated neutralisation of proteolytic enzymes, blocking of excretory, anal and/or oral openings of the larvae by immune complexes, or by prevention of moulting and inhibition of larval development by antibodies against exsheathing antigens. Other enzyme pathways prevent adult worms from optimally producing eggs, or result in abnormal development of certain anatomical structures. Thus *Ostertagia ostertagi* females fail to develop vulvar flaps when grown in immune calves. Similarly, the spicules of *Cooperia* spp. males may be abnormal in immune hosts.

Cell-mediated immunity

Migrating nematode larvae can be considered as functional xenografts ('foreign bodies'), and it is surprising that they are therefore not forcibly removed. This is an indication of their adaptability and adaptation to their hosts. Nevertheless, there is evidence that sensitised T-lymphocytes may successfully attack helminths deep in the intestinal mucosa or in organs in the histotrophic phase. Cell-mediated reactions have been shown to occur in *Trichinella spiralis* and *Trichostrongylus colubriformis* infections. In the former, immunity can be transferred to susceptible animals by lymphoid cells, and, after infection, these animals show delayed hypersensitivity reactions to worm antigens injected intradermally. In the case of *T. colubriformis*, the immunity can be transferred by both cells and serum, and there is a massive lymphocyte infiltration at the site where the worms attach. Sensitised T-lymphocytes depress worm activity, presumably by either the development of an inflammatory response (delayed hypersensitivity) at the site of invasion, or secondly, the release of cytotoxic lymphokines.

Vaccination against helminths

Considering the ineffectiveness of the host response to helminth infestation, it is not surprising that vaccines are not widely available. Experimentally it has been found that irradiated metacercariae can reduce a *Fasciola hepatica* burden in calves. The most important vaccine is that against *Dictyocaulus filaria*, the lungworm of cattle, which is commercially available only in Europe. Second stage larvae are irradiated and 2 doses fed to calves. The larvae penetrate the calf's intestine, but cannot develop to the 3rd stage and therefore do not migrate to the lungs. The exsheathing antigens that are liberated during M2 produce antibodies that are able to block re-infestation. Like the majority of vaccines, this one is not absolute and may break down if calves acquire massive burdens or are otherwise stressed.

Serodiagnosis of helminth infections

Immunological tests are not widely used in the diagnosis of helminth infections, partly because the reaction against the intestinal helminths is not specific, and partly because it is easier, faster and cheaper to examine faeces for the presence of eggs. However, important conditions where ova are not produced, makes it imperative to use serodiagnosis. The conditions are heartworm (*Dirofilaria immitis*) in dogs, visceral larval migrans (*Toxocara canis*), trichinosis (*Trichinella spiralis*), fasciolosis
and *Ancylostoma caninum* infections in humans, and in all these conditions the ELISA test has been shown to be the most useful. Recently, monoclonal antibodies and antibody secreting cell probes have been used in the diagnosis of *Haemonchus contortus* infections in sheep, and Western blot techniques for *Taenia* spp. in dogs and sheep.

**HOST-PARASITE INTERACTIONS – HELMINTH EPIDEMIOLOGY**

**Introduction**

Epidemiology, as per definition, is the study of the interrelationships of the factors that determine the frequency and distribution of a parasitic condition or a disease in a given animal population. Like the infectious diseases, the helminth parasites are also influenced by the epidemiological triad, namely the availability of a susceptible host (Host), the availability of the viable parasite (Agent) and the dissemination of the parasite to the host (Disseminator). Any disturbance between the host, the agent or the disseminator may influence the occurrence of a parasitic condition. As an example: The country is divided into climatic zones or rainfall areas, as indicated in the figure below, because the climate appears to be the single most important factor that can cause a disturbance in the equilibrium of the triad. One would expect helminths to be less numerous in the semi-arid areas, because of climatic conditions. At the same time the host density per unit area, and therefore the carrying capacity is usually low, because of the climate. The summer rainfall area generally has higher rainfall, greater carrying capacity and there are more helminths in the animals. However, one should take into account the climatic preferences of the helminths themselves, some only preferring the winter rainfall area while others occur in one or more climatic zones.
Epidemiological factors that influence helminthoses

Although the reasons for the occurrence of parasitic diseases are multiple and interactive, the vast majority occur because of variation in one or more of four basic reasons. These are summarised in Table and discussed below. This chapter is derived from the excellent work of Urquhard et al., 1992.

1. **An increase in the numbers of infective stages**

1.1 Contamination of the environment

1.1.1 Biotic potential

This may be defined as the capacity of an organism to be a biological success, as measured by its fecundity. Thus, *Haemonchus* and *Ascaris* produce many thousands of eggs each day, while *Trichostrongylus* and *Nematodirus* produce very few (see also Addendum III in the Practical Guide). In the case of the trematodes, the division of the miracidia in the intermediate host is a multiplication division, each redia giving rise to several hundred cercariae. The biotic potential of the cestodes varies considerably, some of the *Taenia* species producing only one larval stage per egg, while *Echinococcus* produces several thousands of protoscoleces per hydatid cyst, which was derived from a single egg.

1.1.2 Stock management

The stocking density can influence the level of contamination of a pasture and is especially important in nematode and cestode infections where multiplication outside the final host does not take place. It has the greatest influence where climates approach the optimum, as in the summer rainfall areas for certain nematodes and the winter rainfall areas for others.

1.1.3 Immune status of the host

The effects of immune status of the host are an important consideration in the epidemiology especially of the nematodes. Young animals are generally less resistant than adults and a preponderance of...
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young animals on a particular farm could easily lead to an outbreak of one or other helminthosis. Ewes, nannys, sows and to a lesser extent, cows, become more susceptible to helminths towards the end of pregnancy and early lactation (the PPRR principle). Parturition in grazing animals is generally synchronised with the climate most favourable for pasture growth, which is also the climate most suitable for the development of the free-living stages of the helminths. The implication is that PPRR ensures increased contamination of pastures when the number of susceptible animals is increasing.

1.1.4 Hypobiosis

The epidemiological importance is that the resumption of development usually occurs when conditions are optimal for the free-living stages and leads to increased contamination of the pastures. It often coincides with parturition, when the female's resistance is low.

1.2 Development and survival of the infective stages

1.2.1 The microhabitat

The ecological requirements of the free-living stages of the nematodes have been discussed above. In addition to optimal climatic factors, soil structure and drainage, vegetation type as well as the formation of a 'mat' of vegetation on the soil (humus, compost), influence the suitability of the microhabitat as far as the survival of the infective stages is concerned.

The mat is well-developed in older pastures and retains sufficient moisture as well as air bubbles to ensure even temperatures and high humidity. The use of rotational grazing with different species of animals and alternating grazing with cultivation reduces the mat and thus parasite survival. In arid areas, pasture growth is negligible and the mat seldom develops. The latter also occurs with overgrazing. Similarly, a high ground water table is important for the development and survival of the intermediate hosts of liver fluke and conical flukes, and thus the survival of these parasites.

The development and survival of helminth eggs or larvae within faeces also depends on temperature and moisture. Cattle dung remains in the original form for much longer than sheep pellets; the moisture trapped inside a dung pat remains for much longer than that in sheep pellets and provides an ideal microhabitat for the nematode larva for weeks or even for months.

1.2.2 Seasonal development

In South Africa, which is essentially a subtropical country, there may be several generations of helminths each year, while in the northern hemisphere, or in countries with distinct wet and dry seasons, the number of generations of helminths may be limited. This is particularly true in the case of those helminths that have a short developmental period, such as the trichostrongyles of ruminants. However, seasonal development depends to a very large extent on optimal climatic factors being present, and these will obviously influence the time of appearance of the larvae on the pastures, the survival rate especially that of the infective stages and, eventually, their numbers.

1.2.3 Stock management
The availability of infective helminth stages is affected by certain management practices. A high stocking density increases the level of contamination and mowing the pastures, i.e. lowering the height of the plants enhances the availability of the infective larvae. Scarcity of grass may cause animals to feed closer to faeces than would normally be the case. On the other hand, shorter pastures are more susceptible to changes in climate and humidity, and hence the free-living stages may be vulnerable. Similarly, the season of parturition may influence the acquisition of helminths significantly. Where lambs or calves are born out of season, the numbers of infective helminth stages are usually low and the chance of infection is postponed to when the animals are older and stronger.

2. An alteration in susceptibility to infection

2.1 Altered effects of an existing infection

This usually occurs in adolescent or adult stock that harbours parasites, but in such numbers that clinical signs are not evident.

2.1.1 Diet

Adequately fed animals are much better able to withstand the effects of helminths than those in poor condition. In the case of *H. contortus*, animals with an adequate dietary iron intake may be able to maintain their haemoglobin levels. During winter, when food is scarce and of poor quality, iron intake becomes insufficient to maintain the haemoglobin levels, with the result that the animals become anaemic and may die.

Factors affecting the epidemiology of parasitic diseases

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<td>Intermediate hosts</td>
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2.1.2 Pregnancy and lactation

When young are born during spring, the greater part of pregnancy falls during winter. Usually, the nutrition is inadequate and this influences the growth and birth mass of the newborn. Under these circumstances, low worm burdens can have a distinct detrimental effect on food conversion of the dam, which often does not produce sufficient milk (often of inferior quality) and which in turn affects the newborn.

2.1.3 Steroid therapy

Steroids are widely used in therapy, and it is known that they suppress the immune system thus altering the host's susceptibility to worms. Egg production by nematodes is increased after steroid therapy and greater pasture contamination occurs.

2.2 Altered susceptibility to the acquisition of new infections

2.2.1 The role of concurrent infections

The interaction of various parasites, or a parasite with another pathogen, results in an exaggerated clinical picture. This is the case with *H. contortus* and *Eimeria* spp. and is perhaps also the case with abomasal and intestinal nematodes in the same animal at the same time.

2.2.2 The effect of chemotherapy

Immunity to parasites is a premunition, implying that the continued presence of small numbers of the parasite stimulates the immunity. If this balance is disturbed, e.g. by administration of anthelmintics, re-infection may occur. A case in point is *Teladorsagia circumcincta*, where removal of the adult worms by anthelmintics results in the arrested larvae being mobilised to continue their development into adults. The resulting adult worm population is often larger than the one that has been removed.

2.2.3 Hypersensitivity

In many cases the immune response to parasites is associated with IgE and a hypersensitivity reaction. Where this occurs in the intestine, increased permeability of the intestinal wall to macromolecules such as protein occurs. This may result in poor growth and poor wool production in immune sheep that are under heavy larval challenge.

3. Parasitism resulting from the movement of susceptible stock to an infected environment
3.1 Absence of acquired immunity

This is adequately illustrated by *Dictyocaulus viviparus* in sheep and the cysticerci of *Taenia saginata* in cattle. Both these parasites elicit a good immunity after the first infection, and in both cases infection of animals not previously exposed to these worms’ results in severe disease in the case of sheep and the excessively high prevalence of cysticerci in the muscles of cattle.

3.2 Absence of age immunity

A significant age immunity develops against relatively few parasites and adult animals not previously exposed to many helminth infections are at risk when introduced into an endemic area.

3.3 Longevity of infective stages

When ecological conditions, e.g. climate, temperature and, above all, humidity are optimal, the infective stages of many worms can survive for extended periods, including those nematodes that develop inside the egg, (*Nematodirus* and the various Ascarids), and those that utilize intermediate hosts. These infective stages are then quite able to infect successive groups of young animals and may cause disease within a few weeks after infections. Where the climate is less favourable, the longevity is not as extended, and only a group of animals will be infected.

3.4 The influence of genetic factors

3.4.1 Between host species

Most parasites show some degree of host specificity and this has been used as an aid in integrated helminth control programmes. For instance, rotational grazing with sheep and cattle or sheep and horses leads to lower infections in both species. On the other hand, some of the economically important parasites are capable of infecting a wide range of hosts which vary in their susceptibility. For example, cattle are more resistant to the effects of *Fasciola hepatica*, which usually kills sheep, and goats seem to be more susceptible to the common intestinal trichostrongyles than cattle or sheep. This has probably to do with the duration of the host-parasite associations.

3.4.2 Between breeds

It has been shown that certain breeds of sheep are more resistant to *H. contortus* than others, while the same breed may be more susceptible to another nematode. However, there are responders and non-responders in every flock or herd, in terms of their ability to develop resistance to internal parasites and it is recommended by some experts that the poorest animals should be culled.

3.5 Sex

There is some evidence that entire male animals are more susceptible to the effects of internal parasites, and this could be important in areas where castration is not routinely done, or where androgens are used to fatten animals.

3.6 Strain of parasite
Helminth infections: Domestic ruminants: Introduction

Strains of helminth that vary in their infectivity and pathogenicity are recognised. The increasing prevalence of anthelmintic resistance of many parasites is to be considered when disease outbreaks occur, especially where control measures are routinely practised.

4. Introduction of infection into a clean environment

4.1 Introduction of new stock

This is certainly one of the easier methods to "import" unwanted parasites, especially when moving breeding stock from one country to another. Quarantine restrictions are poor or non-existent as far as helminths are concerned. Examples are the introduction of *Parafilaria bovicola* into Sweden, either with infected cattle or via infected flies. Similarly, the incidence of heartworm, *Dirofilaria immitis*, has increased dramatically in the United States and Australia with the spread of humans and their pets - the mosquito intermediate host obviously was already present.

In this regard one can consider the introduction of wildlife onto a farm as introduction of new stock. Many helminths of domestic ruminants are transmissible to wildlife and vice versa. This is presumably the way that resistant *Haemonchus contortus* got to infect sable antelope, to the detriment of the latter.

4.2 The role of effluent

The transfer of helminth infections by manure has been reported. In Europe and America, cysticercosis has increased dramatically on farms where human sewage was applied to pastures and the application of pig slurry to pastures grazed by sheep has led to pneumonia due to the migration of the ascarid larvae.

4.3 The role of infected intermediate hosts

Several helminth infections are transmitted by vectors, notably flies, and these may introduce an infection into areas previously free of that infection. Birds may also play a role in disseminating intermediate hosts, e.g. waterfowl that carry the eggs of snails suitable for the *Fasciola* spp. on their feet.

CONCLUSION

These are but some of the factors that should be borne in mind when investigating an outbreak of helminthoses on any farm. It is therefore imperative to obtain as complete a history of the goings-on before even attempting to make the final diagnosis, or to instigate control measures. The identification of nematode eggs is difficult, and takes quite some experience. The best way to make an accurate diagnosis is to culture the eggs, until they have reached the third (infective) stage, and then to compare these larvae with those illustrated in the excellent publication of Van Wyk & Mayhew (2013).

I take the liberty to end with a paragraph from Mares’ (1987) publication: ‘Permanent pastures may perpetuate parasites, but when those permanent pastures are permanently shared as in Africa, then
the cattle eat the sheep worms, the sheep digest cattle worms, and horses mop up both. The over-grazing, periodic droughts and the erosion give the parasites as hard a time as they do the livestock. So, in African Africa, until the fenced farm becomes a reality and management improves, the parasites merely ‘wait in the wings’.

REFERENCES