Paper No. 9.

EPIZOOTOLOGY OF WORM INFECTION.

(With Special Reference to Worms of Domestic Animals).

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It has long been recognized that preventive measures against worm parasites, based on a knowledge of their life-histories and bionomics, are much more expedient than the treatment of infected animals—although the latter may form an important part of such preventive measures. Consequently, in recent years much attention has been directed to the detailed study of life-histories, in the widest sense of the word.

The following types of life-histories, arranged from the epizootological point of view, are found (a few special cases are not included in this scheme):—

I. Eggs leave the host (in faeces, urine, etc.).

(i) Eggs hatch in the free state:

(*a*) Larvae become infective, without intermediate host, e.g., most Strongyles.

(*b*) Larvae pass into an intermediate host (Trematodes) and enter the final host after leaving the intermediate host (*Fasciola*, *Schistosomum*) or with a second intermediate host (*Paragonimus*, *Clonorchis*).

(ii) Eggs do not hatch in the free state:

(*a*) Eggs become infective, without intermediate host, e.g. Ascarids.

(*b*) Further development in and entrance into final host with intermediate host, e.g. Tapeworms, Spirurids (Nematoda).

II. Larvae leave the host, usually intermediate host necessary, e.g. Habronemas of Horse.

III. Larvae remain in host, transmitted by blood-sucking Arthropoda, e.g. Filarias, or transmitted in other ways, e.g. *Trichinella*.

The factors which control the incidence of worm infection are:—

(1) those operating on the free stages of the parasite or on its intermediate host; these are chiefly climatic;

(2) those influencing the chances of the parasite's gaining entrance into the host, which are numerous and widely different in nature;

(3) those acting for or against the successful establishment of the infection, i.e. the conditions which the parasite finds in the host.

These factors apply to any special case in a degree depending on the nature of the life-history; e.g. those with a life-history of Group III type are not affected directly by factors of the first group, only their intermediate hosts may be affected.

These controlling factors can now be considered in greater detail, since an accurate knowledge of them is of paramount importance in the combat against worm infection. But this subject is so enormously wide, that only the main points can be touched on in the following pages.

Climatic Conditions.—The longer the non-parasitic or free-living part of a worm's life is, the less the worm has given itself over to the parasitic habit, the nearer it is still to the free-living forms and the more resistant to the effects of adverse climatic conditions. This is quite true in cases like those of *Haemonchus contortus* and *Oesophagostomum columbianum,* in which the eggs hatch in the free state and the larvae are free-living up to and including the third stage (infective larva), although even in these cases the pre-infective stages cannot resist desiccation. Shortening the free-living period is effected by remaining a longer time in the host (ovoviviparity or viviparity) or in the egg-shell, or by making use of an intermediate host, or a combination of these; but this, either as cause or result, is coupled with loss of resistance of the free-living stages. The eggs and miracidia respectively of *Fasciola hepatica,* for instance, have a very short span of life if climatic conditions are not suitable for hatching or a suitable snail cannot soon be found. Anomalies exist in cases like those of the lungworms, e.g. *Dictyocaulus filaria,* where the eggs hatch immediately after being laid and none of the free-living stages is resistant to desiccation, although the life-history is of the Strongyle type (Daubney, 1920). These worms seem to be badly in need of an intermediate host and are apparently on their way to develop that habit, as is seen from the case of *Aelurostrongylus abstrusus* of the cat; in this case, larvae that are very nearly infective to the cat, still find shelter in mice (Cameron, 1927) and it is conceivable that this is a relatively recent development.

The most important climatic factors affecting worm parasites are temperature and moisture. Although this is usually vaguely realized, some concrete facts may be necessary to make their importance more clearly evident.

Temperature.—Although the fact has been definitely established in a small number of cases only, it may be said that in general there is an optimal temperature for the development of the non-parasitic stages. This temperature varies slightly with the species and lies near 25° C. Above this optimum, development is not so successful and with considerably higher temperatures (say 40° C.) degeneration usually takes place, so that the infective stage is either of low vitality or is not reached at all. The high temperature may act by causing more rapid decomposition of the medium in which the worms develop and may not be detrimental in itself, but in practice as a rule, this comes to the same. At lower temperatures, which are met with more frequently, development is slower or may even practically stop, but death is as a rule not the result, especially in worms with the Strongyle type of life-history. Whereas the infective stage of e.g. *Trichostrongylus instabilis* is reached under an optimal temperature in 60 hours (Mönnig, 1927), it may take several weeks to reach this stage at a low (winter) temperature. The infective stages of this same species, frozen hard for 14 days, are still infective. The same is the case with most species that have this type of life-history and on which such climatic factors chiefly operate. As an exception, the sheep hookworm, *Bunostomum trigonocephalum*, must be mentioned (Cameron, 1923). Temperature alone is thus not a very important controlling factor, but it becomes important in combination with the moisture factor.

Moisture is usually an absolute essential to the free-living, pre-infective stages. These, in the case of *Haemonchus contortus*, *Oesophagostomum columbianum* and other species die immediately on drying. Rare exceptions occur even here; Looss (1911) mentions that eggs of the Strongyles and Trichonemas (Cylicostomes) of the horse, containing complete embryos, developed further on moistening, after they had been dry for six months, but not after nine months. The writer has found a similar resistance in the case of *Trichostrongylus* species of sheep; eggs containing complete embryos are at the moment of writing still able to revive, after having been dry in faeces for over nine months; this is the only pre-infective stage of these worms that is so resistant.

The infective stages of the strongyles usually resist drying to a marked degree; 0.1 per cent. of *H.. contortus* larvae revive after having been dry on glass slides in the laboratory for six months. Also the cercariae of *Fasciola hepatica* have recently been shown to live in hay for about eight months (Marek, 1927). Exceptions occur, which are important to note, e.g. the infective stages of *Bunostomum trigonocephalum* (see Cameron, 1923), *B. phlebotomum* (see Schwartz, 1924), and *Dictyocaulus filaria* (see Daubney, 1920), do not survive drying, and hence infections with these worms are acquired only on moist pastures.

The length of life of the infective larvae in a pasture, which is an important factor, depends to a great extent on their power of resistance against drying. It is well known that the infective larvae of many Strongyles live in the herbage and the surface soil while there is moisture, penetrating deeper down during dry periods. A large proportion will, however, be caught by rapid drying and die unless they are resistant. It is usually stated that the infective larvae of *Haemonchus*, *Oesophagostomum* and *Trichostrongylus* of sheep, for instance, can live about a year in a pasture, while it is understood that favourable conditions are necessary to attain the maximum period. Recent experiments have qualified this statement to some extent by showing that a year of life can be reached only under the most favourable conditions, that this probably happens rather rarely in nature and that the type of soil also plays an important part. It was found that a few weeks of summer temperature without rain sufficed to kill off all the larvae of these species in a very heavily infected plot of black turf soil, while they lived slightly longer in a plot of light, red soil and about 10 months in pots of the same soils which were sheltered and kept moist. (The experimental data underlying this and several other statements made in this article will be published in the Reports of the Director of Veterinary Services). Drying, undoubtedly, plays an important part in these cases, but the high temperature of the soil must be an important factor, stimulating the larvae to greater activity and consequently exhausting their food reserves, since they do not feed.

In connection with the moisture factor, the conformation of the country is important. It will generally be found that hilly country is more worm-infested than flat country, other things being equal, since the valleys between the hills are usually moist and concentration of infection also results here on account of the transport of larvae to the lower levels by rains.

In South Africa wet years and dry years occur frequently, and the helminthologist can find no better lesson on the important rôle of moisture in the life-history of worms than what he can learn by observing the effects of these climatic ups and downs on the incidence of worm infection in the livestock of the country. During wet years the stockfarmers clamour for remedies, and when the dry season comes, everyone finds a " remedy," which " cures " because infection stops and the worms concerned do not live long in the animals. During dry years all the advice given on preventive measures is usually forgotten and the next wet cycle starts the whole problem again.

The greater part of South Africa has a summer rainfall which gives the best conditions, warmth and moisture, for the development of worms. The summer, in this area, is, therefore, the wormy season, while the dry winter is practically a safe period for stock. Even if an occasional shower of rain or a heavy dew or frost may fall in winter, development proceeds so slowly that drying overtakes the larvae before they reach the infective stage. Since the pasture in general is, therefore, safe during the winter, one's attention is focussed on a few unsafe places. These are dams and drinking pools, which are unsafe all the year round. In the first place, they contain the washings of the countryside and the larvae can live in the water for several months. Secondly, at the edges of the water where there is constant moisture and sufficient oxygen, development can proceed, though slowly, and since the animals come frequently to drink and to feed on the green grass that grows here, infection is concentrated and readily picked up.

The winter rainfall area of South Africa, is relatively small and, although worm infection is here not as serious as in the other part, it would certainly be much less if this area was as dry in summer as the other is in winter. Summer rains are more frequent here than winter rains in the other part and, besides, the country is mountainous with many small streams.

A highly interesting condition is found in Bechuanaland. This stretch of country, bordering on the Kalahari desert, and generally considered to be a dry region, is nevertheless heavily worm infested, at least in parts, and even hookworms are quite common. If this region be visited during the dry winter, when many sheep die of worms, it would be difficult to conceive how this is possible. During the summer, when it rains, numerous small, shallow pools or " pans " fill up and hold water for some time. Around these pools the grass remains green when the rest of the pasture dries up, the sheep graze here and drop worm eggs, which find suitable conditions for development, and the resulting conditions are those of an overstocked, wet pasture. When everything is dry again, and the sheep begin to suffer from want of food, the effects of worm infection become evident, but the source of infection is then rather obscure.

The Chances of Reaching the Host.—(i) Moisture and light control to a great extent those larvae of the Strongyle type which migrate up the grass in a dull light and go down for shelter when the surface of the grass dries and the light becomes strong. It is hence a good practice to allow animals to graze only during that time of the day when the sun is well up. The dry winter drives the larvae into the soil and so keeps them away from a host.

(ii) Insanitary conditions are well known to favour worm infection. As examples may be mentioned *Ascaris* infection of pigs, for which a remedy has been devised in the McLean County system of swine sanitation with the purpose of rearing pigs free of infection (Raffensperger 1927, Hall 1928); Ascarids in poultry kept in unclean pens; hookworms in dogs kept in kennels as compared to dogs running free; infection of horses with *Habronema,* which are transmitted through the agency of flies breeding in horse manure and which can be remedied by suitable manure disposal; finally, the watering of animals from dams and pools, which have been mentioned above. It is certain that watering animals from dams is responsible for a large proportion of the worm infection in South Africa. If pure water cannot be given, it is simple enough to fence in a dam and to lead the water into troughs by means of pipes placed not too near the bottom of the dam; this would improve the position considerably. Under insanitary conditions can also be grouped overstocking and permanent pastures. These both tend to concentrate infection and are so obviously favourable to the parasites that they need not be further discussed. It may, however, be interesting here to refer to the findings of Hall (1927) in Central America, where *Haemonchus contortus* and related Nematodes were found to be practically absent owing to wide range grazing and an annual dry, hot season. As a remedy for these evils, methods of pasture rotation have been recommended for many years, which implies that the farm must not be overstocked.

(iii) The ways of grazing of different animals influence the possibility of their becoming infected. The cercariae of *Fasciola hepatica* are known to settle on plants at about water level, and it is recognized that close grazing animals like sheep, are more liable to become infected on moist, fluke infected pastures, than are cattle, which have the habit of grazing high. The same holds in the case of *H. contortus* and related worms, whose larvae hide near the ground in the dense grass for the greater part of the day, while the sunlight is strong.

(iv) The presence and frequence of intermediate hosts, where these are necessary, is obviously of great importance, not only to make development possible, but also to assist the parasite in reaching the final host. As a practical example may be mentioned the fact that fowls running on free range are usually more heavily infected with tapeworms than are fowls kept in even only moderately clean pens, because in the former case the birds have greater opportunities of feeding on the intermediate hosts.

(v) The action of mechanical vectors is important in certain cases. It is well known that earthworms frequently swallow the eggs of fowl Ascarids and tapeworms (*Syngamus trachea*) and, since they are readily eaten by fowls, they serve to bring the parasite to its host. In the case of *Syngamus* this appears to be such an important factor, that earthworms were at one time considered to be necessary and true intermediate hosts of this worm.

(vi) Nematodes like Ascarids and hookworms, which migrate in the body of the host, may cause prenatal infection, and in this way reach a susceptible host through the agency of the mother, who may not be very susceptible herself. The importance of prenatal infection, especially in the case of Ascarids of dogs, is being realized more and more, and it has been found that whole litters of pups may be fatally infected at birth (Shillinger, 1923).

The Chances of Successful Infection.—When the parasite reaches a host, there are several factors which decide whether infection can be successfully established.

(i) The host may be of an unsuitable species, and no infection results; this must happen very frequently.

(ii) Many species of worms can live in several different host species, but usually one of the latter is the most normal or natural host, and the best development is attained in it; e.g. the cystic form of *Echinococcus granulosus* occurs in many mammals, but the cysts are not always fertile, i.e. develop tapeworm heads. In cattle usually 80 per cent. are sterile, while in sheep they are as a rule fertile. The pig Ascaris (*A. suum*) may develop in sheep, but does not attain sexual maturity and is thus infertile in this host.

(iii) In some cases the host species may be correct and susceptible, but even then a large number of parasites do not succeed because they fail to reach the correct organ. In larvae of *Multiceps multiceps*, which enter the bloodstream of the sheep from the alimentary tract, are distributed to all parts of the body, but only those that reach the central nervous system can successfully develop further.

(iv) The number of parasites entering the host simultaneously may have a bearing on the success of the infection. When a sheep swallows a few eggs of *Taenia hydatigena* the larvae pass through the liver to the abdominal cavity and grow into the *Cysticercus tenuicollis*, but when the infection is heavy, the liver may be so damaged that the host dies while the parasites are still quite immature. If lambs become heavily infected with *O. columbianum*, the worms returning from the intestinal wall into the lumen cause such a marked irritation, that diarrhoea results and the majority of the young worms are expelled; this is seen in lambs on the sixth day after infection and the diarrhoea has a typical dark-green colour.

(v) The existence of a resistance to worm infection, also called immunity, is well known, but the exact nature of this quality is rather obscure. In general, it is believed to contain an age factor, but this may possibly only mean that a previous infection has existed, though some experiments seem to contradict this (Herrick, 1925). This is an interesting problem and may in future become important if the cause of the resistance can be more definitely determined. Fernan-Nunez (1927) found that dogs injected with eggs of *Trichocephalus vulpis* became resistant to infection with that parasite for 7-12 months. The injection of lambs with saline filtrates of dried *O. columbianum* by the writer did, however, produce no resistance. Ackert and Herrick (1928) showed that chickens become progressively resistant to infection with *Ascaridia lineata* as they grow older and that one infection produces a strong resistance against a subsequent infection. Sandground (1928), working with species of *Strongyloides*, found that dogs were refractive to reinfection for over six months after having lost a previous infection and that they became refractive to superinfection a few weeks after beginning of the primary infection and before the latter had disappeared. In the case of *O. columbianum* Veglia (1924) found that the development of the parasite in the susceptible lamb differed greatly from its development in the more resistant adult sheep. In lambs the larvae stay in the intestinal wall for about 5 days and then return to the lumen of the intestine, usually without causing any nodule formation. In adult, resistant sheep, a large nodule develops around the larva and many larvae never leave these nodules; the writer found larvae in such nodules more than three months after infection. When the contents of the nodule later become cheesy, and then calcify, the larvae either die there or leave the nodule and wander about between the muscular coats of the intestine, leaving behind them a trace of pus similar to that found in nodules, and only rarely do they pass into the lumen. It appears from most of the available evidence, that, in the case of intestinal worms, the immunity is a local one of the intestinal mucosa and not a general body immunity.

(vi) The general condition of the host is very important in determining the success of the infection and the length of its duration. No better example can be quoted than that of *Trichostrongylus* in sheep; it has been found to be quite impossible to infect good-conditioned, but otherwise perfectly susceptible lambs, with this parasite. Also, if sheep are infected and are allowed to improve in condition the infection is lost immediately. Natural *Trichostrongylus* infection is, therefore, found only in sheep that are underfed or infected with other more virulent worms like *H. contortus*. Although general experience from the realm of bacterial diseases would lead one subconsciously to expect greater resistance in strong, healthy animals, it is difficult to understand this in the case of worms, since the parasite should find more and better food in a healthy host than in a weak one. Possibly it is here, as in the bacterial diseases, a question of the production of antibodies, even though immunity may be only local.

The practical application of this knowledge should be to prevent worm infection by aiming at good condition of the animals, by proper feeding as well as by keeping them free of the most injurious parasites, external and internal, which pave the way for others.

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Paper No. 10.

THE PREVENTION AND TREATMENT OF FASCIOLIASIS IN CATTLE.

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For the control and the complete eradication of Fascioliasis (vel Distomiasis) from our herds and flocks it is firstly essential that we should be acquainted with the habits and bionomics of the fresh water snails which may act as intermediate hosts of *Fasciola hepatica* and *F. gigantica* and, secondly, that we should have a drug lethal to these parasites but practically non-toxic to the vertebrate host.

Dicrocoelium lanceolatum will not be considered because, if present in Africa, it is not of common occurrence and is regarded as practically non-pathogenic to its definitive host.

I. The Invertebrate Hosts and their Habits.

Fascioliasis amongst cattle and sheep in South Africa is limited to those areas where the freshwater snail *Lymnaea natalensis* (Krauss) abound. This mollusc is confined to Africa, south of the Sahara. It is said to be an extremely variable snail and has been described under many names. This species transmits both *F. hepatica* and *F. gigantica*.