Parasitic helminths of the pig: factors influencing transmission and infection levels

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Abstract

The occurrence of parasitic helminth species as well as infection intensities are markedly influenced by the type of swine production system used. The present review focusses mainly on the situation in temperate climate regions. Generally, over the past decades there has been a decrease in the number of worm species and worm loads in domestic pigs due to a gradual change from traditional to modern, intensive production systems. The reasons for some species being apparently more influenced by management changes than others are differences in the basic biological requirements of the pre-infective developmental stages, together with differences in transmission characteristics and immunogenicity of the different worm species. Control methods relevant for the different production systems are discussed. Outdoor rearing and organic pig production may in the future be confronted with serious problems because of particularly favourable conditions for helminth transmission. In addition, in organic farms preventive usage of anthelmintics is not permitted. © 1999 Australian Society for Parasitology Inc. Published by Elsevier Science Ltd. All rights reserved.

Keywords: Helminths; Pigs; Production system; Epidemiology; Transmission; Control

1. Introduction

The helminth fauna of wild boars comprises more than 20 species, of which 5–10 species are particularly common and often co-exist [1, 2]. These helminths may in theory infect domestic swine, yet only outdoor rearing on pasture with a rich soil fauna may lead to a helminth complexity comparable to that of the wild boar [3, 4]. More intensive outdoor management may reduce the number of species considerably, e.g., when well-drained land is used and pasture management is practiced. Indoor rearing of pigs may lead to a further narrowing of the parasite spectrum with only 1–4 species regularly found in permanently indoor piggeries.

It is emphasised that this presentation is not a general description of helminths in domestic pigs world-wide, but deals mainly with the epidemiology and control of pig helminths in the temperate climatic zones, with some examples from Denmark. In this country there is a range of different management systems, yet the industrial-

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ised well-managed indoor systems are dominating. However, during the last decade the number of organic or 'green' swine herds, characterised by poorer hygiene, deep litter systems and outdoor rearing of pigs, have increased. This leads in many respects to a reversion to the traditional pig farming which dominated in the beginning of the century and earlier. The development and survival of pig helminths in the environment are dependent on a number of abiotic and biotic factors. Hence, the management practices determine the transmission rate and the risk of economic losses due to parasitism. In addition, acquisition of immunity is another important factor influencing parasite propagation and worm burdens. Development of immunity may be radically modified by changes in management practices.

Murrell [5] presented an overview of the life cycles and the pathogenesis of the more common helminths of domesticated pigs, while Hale and Stewart [6] discussed the economic impact of parasites and Roepstorff and Nansen [7] described methods for the diagnosis of porcine parasitism. This paper is an extension of a previous review [8] which will focus mainly on important factors associated with the epidemiology and control of helminth species in various production systems.

2. Helminths of major economic importance in domesticated pigs

A list of the most important helminth species in domesticated pigs is presented in Table 1 together with some characteristics that influence their occurrence in intensive and extensive production systems. These helminths are described below, with particular emphasis on the most abundant species.

2.1. Ascaris suum

The large round worm found in pigs has a direct life cycle with a prepatent period of 6–8 weeks. It is characteristic that the parasites are heavily overdispersed within an exposed pig population, and usually only 5–10 adult worms are present in the small intestine if they succeed to establish at all [9]. The prevalence and the intensity of infection appear to be independent of the transmission rate [10–12], and the large number of exposed pigs without patent infection may lead to a considerable under-estimation of the infection rate, i.e. the total number of infected pigs as revealed by positive serological responses in pigs that do not necessarily pass eggs [13]. The adult worms may live for long periods of time [14]. The production of eggs per female seems to be negatively correlated with the size of the worm burden [15], but usually they produce large numbers of eggs (in the order of several thousand eggs per gram (EPG)). Low egg counts (e.g., 100–200 EPG) often represent false-positive counts caused by intestinal passage (coprophagia) of unembryonated eggs originating from infected penmates [10,16], and therefore depends on housing systems and hygiene [17]. Thus, under indoor conditions, ~50% of the copro-positive experimental pigs have been shown to be false-positive [17] and figures from naturally infected fatteners can be of the same magnitude [13].

The shell of the egg is thick and resistant, and the parasites are, therefore, to a high extent protected against desiccation and toxic effects of various chemicals. The eggs of the closely related *Ascaris lumbricoides* may remain viable and infective for at least 6 years in the outdoor environment [18]. Nevertheless, *Ascaris suum* eggs have recently be shown to suffer high mortality under certain outdoor conditions in Denmark (MN Larsen, MSc. Thesis, Copenhagen, 1996). Also, the total lack of transmission from egg-excreting dams to their piglets in intensive indoor Danish sow herds has been explained by a high egg mortality rate due to desiccation [19]. Embryonation and larval development are dependent on temperatures that should exceed 15°C [20], and in temperate regions of the northern hemisphere, development in both the indoor and outdoor environment is mainly restricted to the summer period [15,21,22] (MN Larsen, loc cit), resulting in a higher frequency and density of 'milk spots' in the liver in late summer and autumn than at any other time of the year [22,23]. Below 15°C the eggs are able to survive, but not to

Table 1
Epidemiologically important characteristics of the most important helminths of pigs

Helminth species	Life cycle	Characteristics
Ascaris suum	Direct	Thick-shelled, highly resistant, long-lived eggs—strong acquired resistance ⇒ infection in growers
Oesophagostomum spp.	Direct	Moderately susceptible L3—low, non-protective acquired resistance ⇒ infection accumulate with age
Trichuris suis	Direct	Thick-shelled, highly resistant, long-lived eggs—strong acquired resistance ⇒ infection in growers
Strongyloides ransomi	Direct	Susceptible L3—free-living generations of adults—percutaneous penetration—transcolostral transmission and strong immunity ⇒ infection of piglets
Hyostrongylus rubidus	Direct	Susceptible L3—moderate acquired resistance ⇒ infection of adult pigs
Metastrongylus spp.	Indirect	Earthworm intermediate host—strong acquired resistance ⇒ infection of growers
Stephanurus dentatus	Direct	Susceptible L3—earthworm transport host—long prepatent period
Ascarops strongylina	Indirect	Coprophagous beetle intermediate host ⇒ infection of outdoor pigs
Physocephalus sexalatus	Indirect	Coprophagous beetle intermediate host ⇒ infection of outdoor pigs
Macracanthorhynchus hirudinaceus	Indirect	Coprophagous beetle intermediate host ⇒ infection of outdoor pigs
Trichinella spp.	Indirect	Larvae in flesh—transmission by predation and (crypto-)cannibalism—wide host spectrum (zoonose)
Taenia solium	Indirect	Metacestodes in pigs—man infected by eating raw flesh (zoonose)
Schistosoma japonicum	Indirect	Freshwater snail intermediate host—infection by cercariae—wide host spectrum (zoonose)
Fasciola hepatica	Indirect	Freshwater snail intermediate host—infection by metacercariae—wide host spectrum (zoonose)
Dicrocoelium dendriticum	Indirect	Slugs and ants intermediate hosts—infection by eating ants—wide host spectrum (zoonose)

develop, and the temperature-rise in early summer can therefore result in mass development of eggs accumulated over the preceding winter period under both indoor [15] and outdoor (MN Larsen, loc cit) conditions. Thus, in the northern hemisphere the level of liver condemnation in August has been shown to be strongly correlated with mean temperatures in April–June [23].

Ascaris suum infections may stimulate the development of strong protective immunity [10, 24–27], dependent on the level of exposure and exposure period [28]. Thus, in pigs that have been heavily and continuously exposed over some months, migrating larvae may be killed even before they reach the liver [10, 28, 29]. But often this immunity is not sufficient to protect against infection upon challenge [29], and individual predisposition to harbour adult worms has recently been shown to occur [9]. There seems to be limited age resistance per se, as the larvae easily migrate and establish in parasite naïve baconers and sows [28]. In single-dose infections it has been shown that the number of established adult worms may be negatively correlated to the size of the infective dose [30, 31], while later studies have failed to show any correlation between dose levels and adult worm burdens in both single and trickle infections [10, 12]. In experimental studies it is often questioned whether the inoculation doses used may be unrealistically high. However, a recent study on pasture infectivity using helminth-naïve tracer pigs indicates that 30 kg pigs may pick up a mean of 1000 (range: 250–3350) infective *A. suum* eggs per day (A Roepstorff, unpublished). Practical experience has shown that there is often a poor correlation between uptake of infective eggs, establishment of intestinal worm burdens, presence of specific antibodies and numbers of milk spots in livers, both in natural and experimental infections [10–12, 15, 32–35].

2.2. Oesophagostomum *spp.*

The nodular worms of pigs are usually represented by *Oesophagostomum dentatum* and

Oesophagostomum quadrispinulatum, which commonly coexist. Less common species have been described in certain geographical areas (see [36, 37]). Although nodular worms have a direct life cycle and are common in indoor production systems around the world, they are biologically very different from *A. suum*. The worm burdens in the caecum and colon of experimentally infected pigs may comprise 5000–15 000 adults (e.g. [38–40]), and the number of pre-adults may be much higher [41, 42].

Oesophagostomum infections stimulate low-level immunity which appears to regulate the intestinal load and can reduce the fecundity of female worms [38, 42–44]. Thus, individual females in pigs with low worm burdens may produce ∼10 EPG, while females in pigs with large worm burdens will usually be smaller or even stunted in growth and produce significantly lower numbers of eggs [42, 43]. It is noteworthy that heavily infected sows and pigs may have EPGs of 3000 to 14 000 without showing clinical symptoms [40, 45]. A significant peripaturient egg-rise has been reported in some studies, but this feature is frequently inconsistent or not present at all (see below). It has been demonstrated that the pigs' diet can have a significant influence on establishment and fecundity of *Oesophagostomum* spp. Thus, diets with high levels of insoluble dietary fibres provide favourable conditions for the establishment and egg production of *O. dentatum*, whereas diets rich in digestable proteins and carbohydrates significantly reduce worm burdens and fecundity [46, 47].

Eggs and pre-infective larvae are sensitive to desiccation [48], while the infective third stage larvae are more resistant and may survive for 1 year outdoors [48]. The lower temperature limit for successful larval development is ∼10°C for both species [48], (A Roepstorff, PhD Thesis, Copenhagen, 1986), and eggs deposited on pastures in winter do not, in temperate zones, survive until the spring, like *A. suum* eggs (MN Larsen, loc cit). Some studies have shown that few infective larvae may survive the winter [44, 49], whereas in other studies this has not been documented [50] (H Mejer, LE Thomsen and A Wendt, MSc. Thesis, Copenhagen, 1998).

Interestingly, the prepatent period of *Oesophagostomum* spp. has for many years been claimed to be 6–7 weeks according to general textbooks (e.g. [51, 52]), but several studies have now pointed to prepatent periods of 18–21 days for *O. dentatum* [39, 53, 54], and a recent Danish study has documented that prepatent periods of 17–20 days seem to be the rule for both *O. dentatum* and *O. quadrispinulatum* [55]. Possibly, shorter prepatent periods may be the result of selection as a consequence of modern husbandry factors such as frequent use of anthelmintics, early weaning etc.

2.3. Trichuris suis

The swine whipworm also has some biological features in common with *A. suum*. Thus, it has a direct life cycle with a 6–8 week prepatent period. The larvae develop within highly resistant eggs, in which they may remain infective to pigs for 6 or even 11 years [56, 57]. The infection induces a rather strong immunity [11, 58]. Embryonation of the eggs is, however, proceeding slowly and, although some eggs may become infective within one summer season, most eggs do not seem to reach the infective stage until the second summer in temperate climates [11, 59], (MN Larsen, loc cit). Despite the potential of a long survival time for *T. suis* eggs, recent quantitative plot studies have indicated that egg mortality can be high under certain field conditions, possibly due to biotic and abiotic factors in the soil environment (MN Larsen, loc cit). Often moderate numbers of adult *T. suis* are present in the caecum and colon [11, 60, 61], but the worm burdens may occasionally be high and cause unthriftiness and death [62]. It has recently been demonstrated that severe clinical disease may be associated with *T. suis*-induced suppression of mucosal immunity to resident bacteria [63]. Like *A. suum*, false-positive egg counts may be found, when penmates are infected [64], and low and sporadic *Trichuris* egg numbers can be caused by passage of *T. muris* eggs from mice contaminating the pigs' environment (O Nilsson, pers. com.).

2.4. Hyostrongylus rubidus

The red stomach worm has some features in common with *Oesophagostomum* spp. Pigs are infected by ingestion of free-living L3, and both parasites have short prepatent periods and comparable bionomics [65, 66]. Young pigs may develop a certain degree of resistance to reinfection [67]. Nevertheless, sows may sometimes show rather high worm burdens (e.g. [68, 69]), but faecal egg excretion rates are generally low [70]. The eggs of *Hyostrongylus rubidus* and *Oesophagostomum* spp. are morphologically similar. Thus, diagnosis to the genus level is based on microscopical examination of L3 obtained from coprocultures.

2.5. Strongyloides ransomi

The threadworm of swine has a unique life cycle with free-living generations comprising adult males and females, and parasitic parthenogenetic females in the small intestine. The pigs contract infection orally or percutaneously by infective third stage larvae, and colostral transmission of larvae to the neonatal piglets can occur (see below). The prepatent period is 4–7 days, depending on the route of infection, and the young pig rapidly acquires a strong immunity [71]. Therefore, the faecal egg output may be high for only a short transient period of time, and clinical symptoms occur mainly in the neonatal period. Diagnosis based on faecal egg counts needs to be interpreted with caution. If the faecal samples are not immediately examined or refrigerated, false-negative results may occur as the eggs hatch within 8–12 h at room temperature (20–24°C).

2.6. Metastrongylus spp.

The lungworms of swine include several species, which often coexist, e.g., *Metastrongylus elongatus*, *Metastrongylus pudendotectus*, and *Metastrongylus salmi* (e.g. [72]). They have an indirect life cycle with an earthworm as a true intermediate host [73]. The relatively thick-shelled, resistant eggs embryonate in the external environment, but do not hatch until they have been ingested by an earthworm, in which further development takes place. The eggs in the soil and the infective larvae within the earthworm may remain viable for several years [74].

2.7. Stephanurus dentatus

The kidney worm has a direct life cycle with a long prepatent period of 9 to 16 months. A large number of thin-shelled eggs are passed in the urine. They may rapidly develop to infective third-stage larvae, but the different larval stages are very sensitive to dessication [75]. The L3 infect the host percutaneously or orally, and earthworms may act as transport hosts.

2.8. Less common species

Helminths of domestic swine less commonly encountered in temperate climates include the spiruroid nematodes *Ascarops strongylina* and *Physocephalus sexalatus*, which are harboured in the stomach and have indirect life cycles through coprophagous beetles. The acanthocephalan, *Macracanthorhynchus hirudinaceus*, is a large worm which lives in the small intestine and has an indirect life cycle. The females produce numerous, highly resistant and long-lived eggs which are infective to swine only after development for 2 to 3 months in dung beetles. Most of these parasites are primarily found in the warmer temperates, and especially in tropical and subtropical regions.

Other porcine helminths are important primarily because they are zoonotic. The genus *Trichinella* has recently been divided into several species and genotypes, of which only *T. spiralis* has a domestic transmission cycle and is frequently found in the striated muscles of pigs with diaphragma as one of several predilection sites [76]. Another species, *T. britovi*, is only found sporadically in pigs, and recent studies have shown that this species establishes only in low numbers after experimental inoculation [76], indicating that the domestic pig may not be a usual host. *Trichinella* has a broad spectrum of hosts among the wild fauna, and pigs become

infected by either eating such infected hosts or by eating offal from other infected pigs. Access to outdoor facilities, and thereby to wild or feral hosts, may favour transmission of infection to the pigs, as has been observed in the Baltic countries where large-scale collective farms have recently been substituted by smaller private farms [77]. Humans are infected by ingesting raw, uncooked meat. *Taenia solium*, the pork tapeworm of which man is the definitive host, occurs as the metacestode, *Cysticercus cellulosae*, in the muscles of pigs. As severe clinical disease (cerebral cysticercosis) may be associated with accidental infections of man by the metacestode, this parasite is much more important than its low prevalence rates would indicate. The blood fluke, *Schistosoma japonicum*, which occurs only in the Far East, has a broad host spectrum, including humans, pigs, ruminants, dogs, etc. The adult worms are located in the portal and mesenteric veins associated with the large intestine, and the eggs leave the hosts in the faeces. As for other schistosomes freshwater snails are intermediate hosts.

Other helminths may occasionally be found in domestic pigs. Examples are the liver flukes,

Fasciola hepatica and *Dicrocoelium dendriticum*, the life cycles of which are dependent on one to two intermediate hosts including freshwater or land snails and ants, respectively. Thus, infections are associated with free-range piggeries.

3. Helminths in intensive production systems

Indoor systems, even traditional ones with poor hygiene, exclude worm species with indirect life cycles (Table 2), as their intermediate hosts are absent from their environment. For example, despite *S. dentatus* having a direct life cycle, it is normally not transmitted indoors. This may be due to its long prepatent period in combination with high sensitivity of pre-infective stages to certain environmental factors and/or the absence of transport hosts. Although *H. rubidus* has a direct life cycle and may be capable of transmission indoors [78, 79] this worm is restricted to pigs on pasture [80, 81].

Ascaris suum, *Oesophagostomum* spp., *T. suis*, and *S. ransomi* are all able to successfully complete their life cycles indoors, but many epidemiological surveys have shown that their

Table 2
Helminths found in pigs in relation to type of management

Helminth	Wild boar	Domestic pig		
		Outdoor	Indoor (extensive)	Indoor (intensive)
Ascaris	+	+	+	+
Oesophagostomum	+	+	+	(+)
Trichuris	+	+	+	(+)
Strongyloides	+	+	+	
Hyostrongylus	+	+	(+)	
Metastrongylus	+	+		
Stephanurus	+	(+)	(+)	
Ascarops	+	(+)		
Physocephalus	+	(+)		
Macracanthorhynchus	+	(+)		
Trichinella	+	(+)	(+)	
Taenia	+	(+)		
Schistosoma	+	(+)		
Fasciola	+	(+)		
Dicrocoelium	+	(+)		

prevalence and level of infection are influenced by factors such as hygiene and housing system [61, 82–91]. Nonetheless, this group of parasites is able to be transmitted indoors, but with different degrees of success, presumably as a consequence of their different bionomic characteristics. Thus, *S. ransomi* and *T. suis* seem to be restricted to the most traditional management systems characterised by poor hygiene [91]. In general, at least under Northern European conditions, only *A. suum* and *Oesophagostomum* spp. are successfully transmitted and are prevalent in indoor systems, even though the latter seem to be more sensitive to intensive managemental factors than *A. suum* [89, 90]. Thus, it is difficult, at least in Denmark, to find a swine herd which is free of *A. suum* [19].

4. Worm distribution in pig populations

Helminth infections in the different age groups of pigs in traditional herds are strongly effected/associated with the immunogenicity of the individual species. Two characteristic types of age distribution exist. In one type, the infections usually have a maximum in young pigs, e.g., *S. ransomi* especially in piglets (e.g. [91, 92]) and *A. suum* and *T. suis* especially in young fatteners (e.g. [60, 61, 86, 93]). This pattern of distribution is explained by the highly immunogenic properties of those three parasites. The other distribution type is characteristic for *Oesophagostomum* spp. and *H. rubidus*, which both show higher prevalence rates and intensities of infection in older animals, i.e. the breeding stock [60, 61, 93, 94], which is a reflection of a lower immunogenicity of these two parasites. These patterns are depicted in Fig. 1 that illustrates prevalence rates in three different categories of Danish production systems.

Furthermore, the transmission pattern within a given pig production system has a profound influence on levels of infection in the various age categories (Fig. 1). In small organic farms, pigs are reared largely outdoors, and they are not allowed to be treated prophylactically with anthelmintic drugs [95]. The non-organic herds

(in Fig. 1) relate exclusively to indoor production, and most of these herds are treated routinely with anthelmintics. In this review (Fig. 1), the indoor herd systems are classified as conventional herds, i.e. a wide range of small and large herds with old-fashioned to intensive management, and specific pathogen free (SPF) herds, i.e. generally large herds with modern, intensive management.

The distribution of *A. suum* infection within a given population of pigs varies with type of management. Thus, in the organic farms pigs become heavily infected within their first weeks of life, while in the indoor herds massive transmission is not initiated until early (conventional) or late (SPF) in the fattening period. All surveys to date (e.g. [60, 61, 86, 93]) show that *A. suum* is most prevalent in growing pigs, but in the modern, intensive system the adult pigs (not the younger individuals) have the highest intensity of infection. Indeed, many of the herds within this latter category have a spectacular distribution of *A. suum*, as the pigs do not become infected at all before they are introduced into the breeding stock. Apparently, the piglets do not become infected in the farrowing pens, presumably due to poor embryonation and survival of the eggs in the environment as a consequence of the modern piggery system. Even massive contamination of modern farrowing pens with *A. suum* eggs may not result in infection of piglets [19].

Infections with *Oesophagostomum* spp. are more frequent in adult swine than in young ones (e.g. [61, 85, 93]). The production system determines how early pigs acquire their first infection and how intensively the sows become infected. In the organic farms, the weaners acquire high level infections, which increase with age. However, in the conventional indoor herds, the overall prevalence is considerably lower, while in the indoor SPF-herds the worms are almost absent from all age groups except boars, which have low levels, possibly as a consequence of holding them in rather traditional pens, even in intensive herds.

In the organic farms, *T. suis* occurs most frequently in the weaners, but egg counts are generally low, while in indoor herds this parasite is found rather sporadically, apparently without
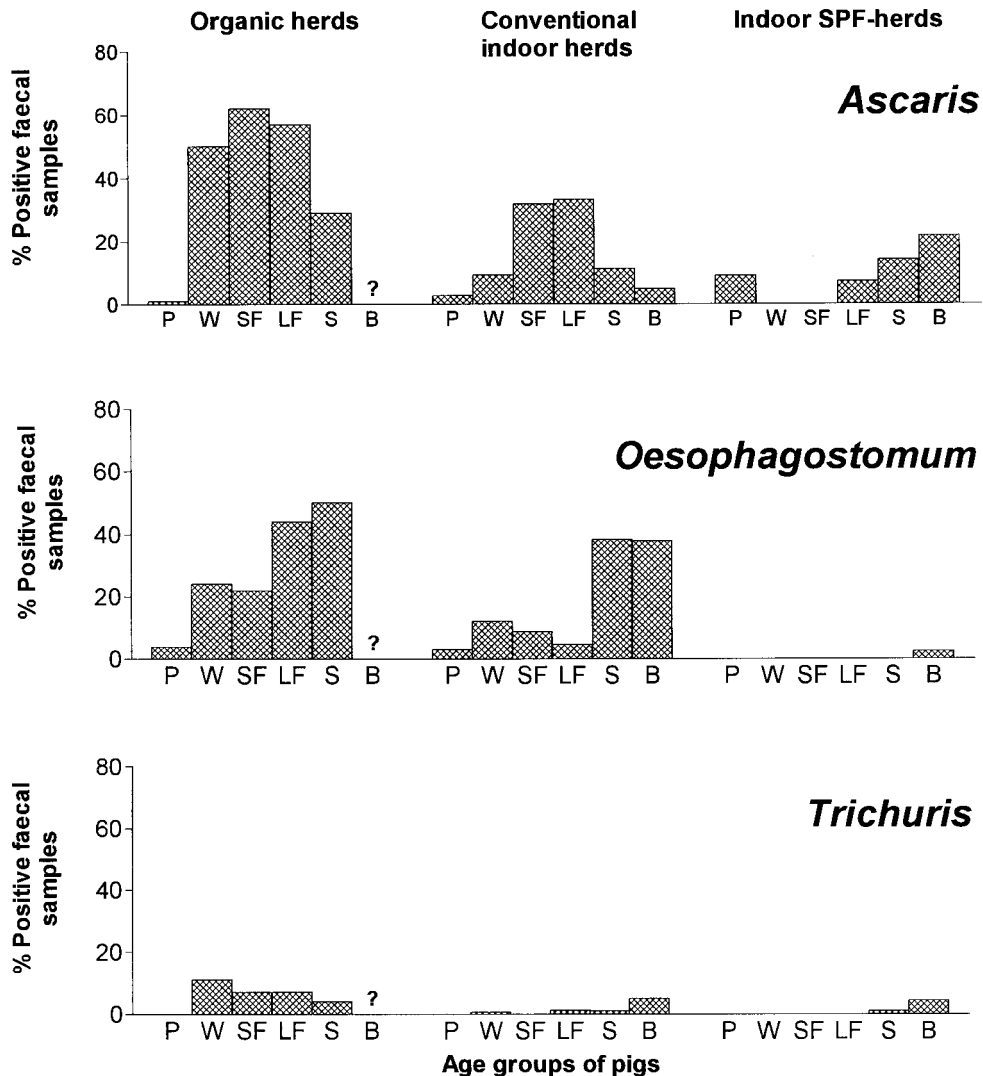
Fig. 1. Prevalence (% positive faecal samples) of *Ascaris suum*, *Oesophagostomum* spp., and *Trichuris suis* in Danish sow herds with different management systems. The pigs of the organic herds had access to outdoor facilities, and when present indoor pens were very traditional and no anthelmintics were used in these herds (data from [95]). The specific pathogene free (SPF) herds had undergone a throughout sanitation which, however, normally do not eradicate helminth infections. The low infection levels are most likely caused by the very intensive housing systems that are generally used in SPF-herds (data from [93]). Abbreviations: P: piglets max. 5 weeks old; W: weaners; SF: small fatteners; LF: large fatteners; S: sows; B: boars; ?: no samples. Note the false positive *Ascaris* egg counts in the piglets (see [17]).

preference for a specific host age group. *Strongyloides ransomi* has been recorded in Denmark but at very low levels [45, 93], and knowledge about distribution patterns in various production systems is inconclusive.

5. Vertical transmission

Vertical transmission is an important adaption of parasites to the host to ensure that the next host generation becomes infected. Pig helminths

seem to have adopted several different strategies. *Ascaris suum* infections stimulate, as mentioned, a high level of acquired resistance. It has been suggested that immunity may be transferred passively from infected sows to their offspring with colostrum [96]. However, recent results seem to indicate a much more complex relationship. Thus, long-term experimental exposure of sows seems to induce some tolerance in piglets to infection (J Boes, pers. comm.). The latter observation may have interesting epidemiological implications if it can be confirmed under natural conditions, since heavy long-term infections of a parent generation may then increase the risk for higher worm burdens in the next generation. A possibility for migrating *A. suum* larvae to cross the placenta in pregnant sows should also be considered, although attempts to show such transmission have so far failed [97, 98]. As indicated previously, *Oesophagostomum* spp. most frequently occur in adult pigs, and a significant peripaturient eggrise can last for an entire lactation period [99, 100]. However, most often the egg rise is inconsistent or does not occur at all (e.g. [45, 93, 101]), suggesting that the overall epidemiological role of this phenomenon may perhaps be of minor relevance. In traditionally-managed herds, sows may nevertheless be the most important source of infection to piglets, which is the reason for including a strategic anthelmintic treatment of the sows before they are moved to the farrowing pens. There is no current evidence for vertical transmission of *T. suis*, but it would appear that the longevity of the eggs may make such a transmission mode less important. The threadworm, *S. ransomi*, utilises a very efficient vertical transmission route, as larvae in the sow's tissue may be activated shortly prior to farrowing and transferred to the neonatal piglets via the colostrum [102]. Also, prenatal infection in the pig has recently been described for the zoonotic trematode, *S. japonicum* [103]. It was shown that all of the 26 piglets born by sows experimentally infected with *S. japonicum* during week 10–11 of gestation were born with patent infections. It is also possible that *Trichinella spiralis* can be transmitted by the transplacental route, as it has been shown

recently that guinea pigs may be infected *in uteri*, while an attempt to infect piglets in the same manner has failed (P Webster, pers. comm.).

6. Control measures against helminth infections

Pigs in modern and highly intensive pig production systems (Fig. 1) are usually infected with few worm species at low intensities [19, 104]. Such herds have a high level of hygiene, and often pigs of all age categories are kept on slatted floors without bedding or straw. In addition, dry sows are mostly tethered. Under such conditions faecal deposits will drop away from the pigs and the conditions for eggs to embryonate may be inadequate. Therefore, the contamination level and transmission rate may be rather low, and anthelmintics applied at regular intervals may have little or no additive effect [19]. In herds with higher parasite transmission rates, such as traditionally managed herds, proper worm control may be based on improving the hygienic standard combined with the usage of anthelmintics. However, routine anthelmintic dosing appeals to pig farmers for reasons of convenience [105], and it may be the only control measure carried out. The effect of each treatment may be transitory, if the pigs are reinfected continuously [15], and it has been difficult to find statistical differences between prevalence rates in herds with and without anthelmintic treatment regimens, particularly in relation to *A. suum* infection [83, 85, 88, 89]. Under extensive conditions on pastures, the principles of worm control in ruminants, already in routine use for many years [106], may be attempted. These principles include turn-out on uncontaminated pastures, pasture rotation, mixed or alternative grazing with other animal species, and the integrated use of anthelmintics (e.g. [5]). Such integrated control programs have been very effective in practice [107, 108]. Again, it is worthwhile emphasizing that anthelmintic treatment alone may not completely control the helminths, since the animals will inevitably be reinfected on the contaminated pastures, and the anthelmintic effect may, therefore, be rather transitory [61, 109]. The observation that

Oesophagostomum spp. do not always survive the winter on pastures may suggest that effective anthelmintic treatment(s) of all pigs in an outdoor herd in winter may eliminate the parasite from a herd. Another direct host-related control measure is to ring the snouts of the sows, as this will reduce their rooting behaviour and consequently the uptake of infective eggs and larvae from the soil. An even more specialised method is the 'gilt only' method [110], in which sows are allowed to farrow only once before they are slaughtered; this may effectively control *Stephanurus dentatus* because of the long prepatent period of this parasite. However, in all production systems, except in organic farms, regular use of anthelmintics alone is the most common control method, unfortunately sometimes the only control intervention. A number of broad and narrow spectrum anthelmintics for treatment of nematodosis in pigs are widely used [105, 111]. There are two different principles of control, namely treatment of sows or groups of pigs individually at specific times, i.e. strategic treatments adjusted to age and reproductive cycle, or treatment of all pigs in the herd at specific times of the year. In the former, sows are treated 1–2 - weeks before farrowing, often followed by a move to clean farrowing units. The objective is to eliminate worm burdens from the sows to prevent contamination of the environment of the newborn piglets. To reduce possible further transmission of infection, piglets may again be treated at weaning and once or twice during the fattening period. Examples of such strategic programmes are the North Carolina Parasite Control Program [112] and the McLean County Sanitation System [113]. The other principle involves all pigs in the herd being treated at selected times of the year. This is not based on parasite transmission patterns, but merely on labour-saving and cost-cutting technical reasons. Nevertheless, in herds without transmission in the farrowing pens, treatment of the infected age groups every half year may be recommended.

7. Anthelmintic resistance

Where anthelmintics are used excessively and repeatedly, anthelmintic resistance may gradually develop. The general subclinical nature of helminthosis in the pig may explain, however, why drug-resistance has not been revealed on clinical grounds. Anthelmintic-resistance was first identified in pig parasites in Denmark, where resistance to pyrantel was observed in a mixed population of *O. dentatum* and *O. quadrispinulatum* [114]. *Oesophagostomum dentatum* was slightly more resistant than *O. quadrispinulatum* and female worms were in general more resistant than males [115]. Later, resistance to levamisole was demonstrated, but this was confined almost exclusively to a particular isolate of *O. quadrispinulatum* [54]. This isolate, which had not previously been exposed to pyrantel, exhibited significant cross-resistance to pyrantel. In contrast, the pyrantel-resistant isolate identified in 1987 was almost fully susceptible to levamisole. This uni-directional cross-resistance is in accordance with findings for resistant *Trichostrongylus colubriformis* of sheep [116, 117]. To the extent that these observations generally hold true, the strategic choice of an anthelmintic becomes decisive. If, for example, pyrantel is used until resistance develops, then levamisole will still be effective, but if these drugs are used in the opposite order, the use of levamisole may pave the way for the simultaneous development of resistance to both drugs. Recently, resistance of *O. dentatum* to pyrantel, levamisole and ivermectin has been induced experimentally, while no resistance could be induced to fenbendazole, which continually proved to have a high efficacy (H Bjørn, unpublished). A recent survey on the prevalence of anthelmintic resistance in Danish sow herds revealed several cases of resistance in nodular worm populations, including one herd with fenbendazole resistance (A Dangolla, PhD Thesis, Copenhagen, 1994), but to date there are no published reports on drug resistance in any other pig helminth, including *A. suum*. When frequent treatment with the same drug is given over several consecutive years, the potential for *Oesophagostomum* spp. to develop anthelmintic

resistance may be high due to the high number of worms in the intestine upon which resistance may be selected and the relative short-lived free-living larvae, and the short generation time [118]. In comparison, *A. suum* may for theoretical reasons be a much poorer candidate for the development of anthelmintic resistance due to the small intestinal worm numbers and the large extra-host refugium of parasites, i.e. non-embryonated and embryonated eggs, which is not exposed to the drug at the time of treatment. The type of husbandry system, intensive or extensive, may determine the degree of development of anthelmintic resistance. In large-scale, intensive indoor systems drug treatments are often given at frequent intervals, and the parasite refugium is relatively small due to the daily removal of faeces and the dry environment. This may favour an earlier and stronger development of drug resistance than in extensive outdoor systems where the refugium may be large and could persist for longer periods of time.

8. Future control strategies

Worm control in the modern pig industry should be based on better understanding of the parasitological status and the transmission capacity in the individual herd [119]. Significant interrelations have already been established between extrinsic factors, and parasite prevalence and intensity, and it should be possible on the basis of herd records and routine surveys (e.g. coprological surveillance) to select appropriate additional control measures, e.g. in the form of strategic drug regimens. Or there may be situations where treatments may no longer be necessary [19]. In the extensive outdoor system, helminths may be expected to be present at a level which may argue for invention, e.g., in the form of a combined system of pasture management and strategic drug treatment. In certified organic farms in Denmark, preventive use of anthelmintics is not permitted. These farms, which at present are growing in number, must rely on management strategies such as pasture rotation or even biological control against some nematode worms etc.

The possibility of biological control of animal parasitic nematodes by use of nematode-killing microfungi has received increasing attention (see [120]). For the practical use of these microfungi as biological control agents, deposition of the fungal material should preferably be in the dung, where the entrapment and killing of pre-parasitic larvae take place. After a series of careful laboratory selections of fungi there is now a number of species available (e.g., *Duddingtonia flagrans*). Such fungi exert a significant nematode killing effect in dung after having survived passage through the alimentary tract of calves fed the fungi. Promising field investigations have been conducted on grazing calves [121, 122], and the selected isolates are also capable of passing the alimentary tract and killing nematode larvae in both the horse [123] and pig [124]. With regard to the latter species, significant reductions of 87% and 70% were demonstrated in the parasite populations of *O. dentatum* and *H. rubidus*, respectively [124]. However, the egg-dwelling parasites *A. suum* and *T. suis* are not attacked by the above group of fungi, because *D. flagrans* and related fungi only kill free-living, mobile larvae. Studies on specific egg-parasitic microfungi have been initiated.

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