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Aggregation of *Taenia solium* cysticerci in pigs: Implications for transmission and control

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ABSTRACT

Parasite aggregation within hosts is a fundamental feature of parasite distributions, whereby the majority of parasites are harboured by a minority of hosts. Parasite aggregation can influence their transmission and hence control. In this narrative review, possible sources of aggregation of *Taenia solium* cysticerci in pigs are discussed, along with implications for control of the parasite. While heavy *T. solium* infections in pigs could most likely be associated with ingestion of high doses of infective parasite eggs, consistent with coprophagic behaviour of pigs, lighter infections indicate a role of indirect routes of transmission to pigs, mostly from lower infection doses. Light infections are likely to be missed by commonly used diagnostic methods - tongue examination or meat inspection - and end up in the food chain. Hence, they entail a 'hidden' risk and are of a particular public health concern, especially in areas where meat is consumed raw or undercooked. To be effective and sustainable, control strategies against *T. solium* likely require a broader understanding of, and consideration for parasite transmission dynamics. More importantly, a holistic One Health approach incorporating interventions on humans, pigs and the environment will likely have a larger, more successful and sustainable impact.

1. Introduction

The impact of macroparasites on host populations depends on the parasite frequency distribution (Gulland, 1995; Roberts et al., 1995). The distribution is a function of spatial distribution of hosts and distribution of parasites within hosts (Cohen et al., 2017). Aggregation of parasite populations among host populations is one of the intrinsic features of host-macroparasite interactions such that relatively few hosts harbour the large majority of parasites while many hosts harbour few or no parasites (Crofton, 1971; Poulin, 1996; Shaw et al., 1998). Parasite aggregation is influenced by factors that cause heterogeneity in host susceptibility (intrinsic factors) or in host exposure/predisposition (extrinsic factors) (Anderson and Gordon, 1982; Poulin, 2006). Heterogeneity in susceptibility refers to

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the immune response following an infection. Extrinsic factors dictate the extent to which an animal will be exposed to infective materials and include factors such as environmental factors, agents that disperse eggs into the environment, animal feeding behaviours and farming practices. Host heterogeneity in parasite intensity strongly influences establishment and subsequent spread of parasites.

The pork tapeworm *Taenia solium* constitutes a serious socio-economic and public health problem particularly among impoverished rural communities in sub-Saharan Africa, Latin America, and South-east Asia. The parasite is responsible for taeniasis-cysticercosis, a zoonotic disease complex affecting pigs as intermediate hosts (porcine cysticercosis) and humans as final hosts (taeniasis) and inadvertent intermediate hosts (human cysticercosis). Humans acquire the adult stages of the parasites through consumption of insufficiently cooked (or raw) pork containing the parasite's larval stages (cysticerci). Pigs get infected and develop cysticercosis when they ingest infective parasite eggs released through faeces of people who harbour *T. solium* tapeworms. This happens either directly through coprophagy or through contaminated feed or water. Human cysticercosis develops when humans ingest parasite eggs through a faecal-oral route, with cysticerci found in the skeletal, ocular, or neural tissues. Cysticercosis of the brain is called neurocysticercosis (NCC); and is the most severe form of the disease, considered the major cause of acquired epilepsy in endemic countries (Debacq et al., 2017; Gripper and Welburn, 2017; Ndimubanzi et al., 2010).

The burden of cysticercosis is estimated to be 2.8 million Disability-Adjusted-Life-Years (DALYs) making *T. solium* the foodborne parasite with the highest burden globally (Torgerson et al., 2015). Infection in pigs disproportionately affects poor farmers and their communities, who succumb to income losses due to reduced market value or condemnation of infected pigs/carcases. While taeniasis/cysticercosis is considered to be a 'tools ready' disease (WHO, 2007) and potentially eradicable since 1992 (CDC, 1993), its control has remained a challenge. No cost-effective intervention strategy has so far been validated for use in the field and sustainability of impacts of many intervention options remains to be demonstrated (Carabin et al., 2018; Johansen et al., 2016; Carabin and Traoré, 2014).

Like for other parasites, feasibility, efficacy and sustainability of control strategies against *T. solium* require a clear understanding of the transmission dynamics, which are based on, among other things, the interaction between the host, the parasite and the environment. As far as the spatial distribution of hosts is considered, several studies have reported spatial clustering of pigs and humans infected with *T. solium*. Porcine cysticercosis has been found to strongly cluster around households with tapeworm carriers (Lescano et al., 2019; O'Neal et al., 2012; Pray et al., 2017; Sarti-Gutierrez et al., 1988); while cases of taeniasis have appeared to cluster around the location of infected pigs (O'Neal et al., 2012; Pray et al., 2017; Sarti-Gutierrez et al., 1988). It is unknown how much these hotspots contribute the overall transmission; and to what degree this transmission varies depending on settings.

As for parasite distribution within hosts, studies have demonstrated the presence of aggregation of *T. solium* cysticerci in slaughtered pigs (Chembensofu et al., 2017a; Huerta et al., 2001; Kabululu et al., 2020b; Sah et al., 2017; Sciutto et al., 1998b). This paper discusses intrinsic and extrinsic factors which could influence the observed aggregation of *T. solium* in pigs; together with the implications that the aggregation could have on the transmission and control options for *T. solium*.

2. Discussion

2.1. Direct human to pig transmission: acquired concomitant immunity

The most seemingly obvious means of transmission of infective eggs to pigs is through direct ingestion of human stool from a tapeworm carrier. The resultant parasite intensity will depend on the ingested dose of infective eggs and the strength of the host immune response. For simplicity, it is hypothesized that four scenarios will dictate the infection intensity following a direct ingestion of stool from a tapeworm carrier;

1. An ingestion of a relatively high dose of infective eggs followed by a relatively weak immune response will result to a heavy infection intensity.
2. An ingestion of a relatively high dose of infective eggs followed by a relatively strong immune response will result to a moderate/light infection intensity.
3. An ingestion of a relatively low dose of infective eggs followed by a relatively weak immune response will result to a light infection intensity.
4. An ingestion of a relatively low dose of infective eggs followed by a relatively strong immune response will result to no infection or a light infection intensity.

While ingestion of a relatively high amount of infective eggs (scenarios 1 and 2) can be associated with direct ingestion of faeces released by a tapeworm carrier, ingestion of a relatively low dose of infective eggs (scenarios 3 and 4) is probably a result of an indirect ingestion of infective parasite eggs.

A heavy infection can be assumed to be resulting from an ingestion of either a single high dose of parasite eggs or superinfection, which is defined as an accumulation of an increased infection intensity due to repeated exposures to small doses of infection. However, among the taeniid cestodes, studies have demonstrated presence of acquired concomitant immunity whereby an animal infected with metacestodes (larval stages of the parasite) is immune to reinfection while at the same time parasites from the initial infection remain unaffected (Lightowlers, 2010). This prevents development of superinfection and has been demonstrated in a number of experimental infections with other taeniid cestodes (see reviews by Lightowlers (2010) Lloyd (1987), Rickard and Williams (1982) and Williams (1979)). The immunity results from exposure to the early developing parasite, which stimulates a protection against the survival of parasites from a subsequent exposure to eggs (Heath, 1973). In a study by de Aluja et al. (1999), this immunity was shown to persist for a period between five and nine months following an experimental infection with *T. solium* eggs. Longer duration of the immunity was shown with other *Taenia* species. For example Heath and Chevis (1978) showed that the immunity can persist for up to 14 months in rabbits experimentally infected with *T. pisiformis.* Therefore, based on the results of the studies presented above, it seems likely that heavy *T. solium* infection intensities in pigs result from a single ingestion of a very high dose of *Taenia* eggs. In support of the first hypothesis presented above, to result in a high intensity of infection, ingestion of a high dose of *Taenia* eggs is likely followed by a relatively weak immune response. This proposition is corroborated in a study by Santamaría et al. (2002) who demonstrated in an experimental infection study that immune responses were more efficient in pigs infected with low doses of *T. solium* eggs, such that those pigs had relatively more degenerated cysticerci compared to pigs challenged with high doses of eggs.

Ingestion of a very high dose of *Taenia* eggs is consistent with the coprophagic behaviour of pigs. Coprophagy is enhanced by free roaming of pigs, unless pigs are deliberately provided with human faeces, or defaecation practiced within the pig confinement area (Flisser et al., 2003; Nguekam et al., 2003).

2.2. *Direct human to pig transmission: age predisposition to infection*

Findings of an experimental infection study by Deckers et al. (2008) showed that the number (and proportion) of viable cysticerci decreased with the age at which the animals were infected. The same age disposition was observed in an earlier study by de Aluja et al. (1996) which showed that older pigs were more resistant to infection; and a study by Sciutto et al. (1998b) which suggested that younger animals were less able to generate an effective immune response against the parasite.

In addition, a social hierarchy has been reported to exist among free ranging pigs, which results to dominant adult pigs ingesting faeces more frequently than less dominant young pigs. This means that adult pigs are more exposed to infective materials compared to young pigs (Copado et al., 2004; Gonzalez et al., 2006; Sciutto et al., 1998b). Previous studies in Mbeya Rural and Mbozi districts seem to corroborate this observation by reporting significantly more cases of infection among older pigs (Braae et al., 2016; Braae et al., 2014; Komba et al., 2013). However, in these studies serology was used for diagnosis and estimates of infection intensity were not determined. Poudel et al. (2019b) undertook a study to relate the prevalence of cysticercosis in individual naturally infected pigs with the animal's age, and based data on comprehensive necropsies. It was found that occurrence (and probably intensity) of infection did not increase in animals beyond 7–9 months of age. It was concluded that animals older than approximately 1 year of age may be relatively resistant to *T. solium* infection. In the study by Kabululu et al. (2020b) where aggregation of cysticerci was also reported, specific ages of the slaughtered pigs were not recorded and therefore it could not be determined if there existed any association between cysticerci intensity and age. The study showed that at least 70% of the pigs were kept in pens or were tethered; and although it was not reported in the paper, free roaming was more observed among younger pigs than adult ones. This, for example, included piglets of a sows which were tethered, and therefore were free to wander around or piglets/weaners which could find their way out of pens through spaces on the walls, which would otherwise be too large for bigger adult pigs.

Hence, findings of the studies presented above suggest that heavy infections more likely result from infection at an early age, by ingestion of a high dose of infective materials consistent with direct ingestion of faeces from a tapeworm carrier. This seems to support the first hypothesis, especially on the fact that young pigs are a more likely to have a weaker immune response, leading to a high infection intensity upon ingestion of a massive dose of infective materials. On the other hand, the fact that young pigs are less likely to ingest faeces compared to adult dominant pigs is among the possible explanations as to why there is relatively few pigs with massive numbers of cysticerci.

2.3. *Direct human to pig transmission: risk associated with 'open' latrines*

In many endemic areas, transmission of infection to pigs has been largely associated with coprophagic behaviour of free roaming pigs (Komba et al., 2013; Pondja et al., 2010; Sarti et al., 1992a; Sikasunge et al., 2007) and human outdoor defaecation (Braae et al., 2015; Jayashi et al., 2012; Ngowi et al., 2004; Sarti et al., 1992b). Hence, it seems feasible to interrupt transmission by increasing latrine coverage and limiting pig free roaming.

In a study by Kabululu et al. (2020b), about 20% of pigs in Mbeya Rural and Mbozi districts were observed to be freely roaming. However, although latrine coverage and use was reported to be relatively high (95.4% and 99.1% respectively), about 45% of the latrines could be accessed by pigs. A study in northern Tanzania by Kavishe et al. (2017) reported that human stool on the latrine floor was a common sighting. The situation could be the same in other pig rearing rural communities in Tanzania, and elsewhere. Pig foraging on the faecal material from latrines has previously been reported in Latin America (de Aluja, 1982) and in Asia (Nemeth, 1989). It is likely that faecal matter on the floor of pit latrines will be in relatively smaller quantities. As demonstrated by Santamaría et al. (2002), pigs foraging on faecal matter on the floor of open latrines will most likely result to light infections, as also suggested in the third (and probably fourth) hypothesis put forward in this paper.

2.4. *Direct human to pig transmission: variability in egg shedding*

Direct ingestion of stool released by a tapeworm carrier will not necessarily result to a heavy infection. One of the possibilities is the reflected in the first hypothesis put forward above, that is, a strong immune response following ingestion of a high dose of infective materials. Another possibility is the variability in the excretion of gravid proglottids with infective eggs from day to day (Ito et al., 2020). This would indicate that during some days, stool released by a tapeworm carrier will contain few infective eggs which will lead to an infection with a few viable or mostly degenerated cysticerci, or no infection at all. The day -o-day variability in the expulsion of eggs from tapeworm carriers coupled with the relatively low prevalence of taeniasis (usually between 1% to 3%) in *T. solium* endemic areas partly explain the aggregation of *T. solium* cysticercosis (Coral-Almeida et al., 2015).

2.5. Indirect human to pig transmission: the role of egg dispersal

Due to the immotile nature of the *T. solium* proglottids, eggs and proglottids are likely to be ingested at the site of deposition, signifying a more important role of direct ingestion of faeces in the transmission of eggs. However, several studies have suggested several ways by which eggs could be dispersed from the site of deposition, which in turn determine different ways and scale by which the eggs will be ingested by pigs. Overall, infections resulting from ingestion of infective eggs dispersed from the site of deposition will most likely result to light infection intensities. Cases of porcine cysticercosis have been reported in areas considerably distant from households with tapeworm carriers, which does imply, among other things, the role of dispersal mechanisms such as rainfall and arthropods.

Rainfall seems to play a significant role in the dispersal and survival of *Taenia* eggs and hence transmission of the parasite. The effect of water current during the rainy season in mediating egg distribution was previously suggested by Sciutto et al. (1998b). A study in Mexico by Copado et al. (2004) observed a significant seasonal difference in transmission to pigs, where free ranging pigs were observed to ingest human faeces less frequently during the wet season. Two reasons were put forward, readily availability of other food sources during the wet season, and washing away of faeces by rain. The latter reason was also suggested by Maganira et al. (2020) who found that *T. solium* DNA in soil was detected exclusively during the dry season in Kongwa District, central Tanzania. A study by Storey and Phillips (1985) showed that rain was able to wash *Taenia saginata* eggs into the soil where they were protected against radiation and desiccation. Hence, apart from dispersing the *Taenia* eggs, rain could also contribute to the survival of the eggs.

Seasonal fluctuation in prevalence of *T. solium* cysticercosis has also been suggested from serological surveys carried out in Mbeya Rural and Mbozi districts (Braae et al., 2014; Kabululu et al., 2018). Both indicated that transmission was higher during the dry season. In the areas, pigs are more confined during the wet season, which is also the cropping season, so as to prevent them from ravaging the crops in the fields. Hence, the period of high transmission coincided with the period when more pigs were left to scavenge (post-harvest/dry period). In addition, there is less work in the fields during the dry season as compared to the wet season, which means more defaecation is done close to home where pigs spend most of their time (Thomas et al., 2013). Therefore, although direct ingestion of faeces in the fields was less frequent during the rainy season, on the other hand it implies that the eggs would be more dispersed in the environment, with an increased likelihood of lighter infections to more pigs.

The extent of environmental contamination is influenced by the degree of egg shedding from tapeworm carriers, rate of dispersal, and survival of the eggs in the environment (Gemmell, 1987; Torgerson and Heath, 2003). In endemic areas, it is assumed that there is high egg output from tapeworm carriers which leads to high environmental contamination (Flisser, 1994). A household survey in a Mexican rural community reported a high presence of *Taenia* eggs (25.3% of soil samples) by using direct microscopical examination of the superficial layer of soil which indicated a high degree of environmental contamination which is crucial in egg dispersal (Huerta et al., 2008). However, no distinction was made between different species of *Taenia*; hence it was impossible to ascertain the proportion of *T. solium* eggs. In the study by Maganira et al. (2020), a relatively lower level (3.1%) of soil contamination by *T. solium* eggs was detected using droplet digital polymerase chain reaction (ddPCR) and it was suggested that pigs in the area acquire cysticercosis mainly by direct consumption of eggs in human faeces rather than from contaminated soil. Absence of soil contamination in the rainy season was associated with the possibility of rainwater washing off the eggs into surface water such as streams and rivers. With high dispersion of eggs in the environment, the chances of indirect ingestion of eggs are increased, most likely through contaminated water and feed, as suggested by Braae et al. (2015) and Komba et al. (2013). Further, a study in Mbeya by Msoffe (2019) assessed intestinal parasitic helminths eggs concentration and profile from samples of wastewater and vegetables irrigated with wastewater. It was found that about 75% of vegetables irrigated using reused wastewater were contaminated with helminth eggs. A quarter of the eggs were identified to be *T. solium* eggs by using multiplex PCR. Consumption of such contaminated vegetables presents a risk of infection, more so if they are consumed raw or undercooked, as it was reported in the study.

Arthropods, particularly flies and dung beetles, have also been reported to play a role in transmission of *Taenia* spp. [see a review by Benelli et al., 2021]. For example, Bílý et al. (1978) described evidence for the transmission of eggs of *T. saginata* by various species of beetles. Subsequently, it was shown that dung beetles may contribute to dispersion, and hence transmission of *T. solium* eggs to pigs in endemic areas (Arriola et al., 2014; Gomez-Puerta et al., 2014).

As pointed out above, transmission through egg contamination in the environment depends on the survival and viability of the eggs in the environment. However, a few studies have tried to investigate survival and transmission of *Taenia* eggs in the environment [reviewed by Jansen et al., 2021]; and many of the studies did not quantify the material (water or soil) used and the eggs were not identified to the species level. Overall, humidity and temperature have been identified as the major factors determining survival of *Taenia* eggs in the environment, with humidity affecting the survival of eggs more than temperature. Eggs' survival seems to be favoured by moderate temperatures (5–25 °C) (Froyd, 1962; Willis and Herbert, 1984) and relatively higher humidity (> 34%) (Laws, 1968).

A study which assessed transmission potential of *T. saginata* eggs showed that the eggs could still be viable at 20 °C after four and two months in water and silt, respectively (Bucur et al., 2019). In low temperatures of the temperate regions, *T. saginata* eggs have also been shown to remain infective for up to six months (Bucur et al., 2019; Ilsøe et al., 1990). In general, in the field and under optimal conditions, *Taenia* eggs can survive for up to 1 year (Duthy and van Someren, 1948). The reported long survival increases a chance for the eggs to infect new hosts and therefore signifies the potential role of the environment in the transmission of *Taenia* spp. However, an important caveat is that, while some eggs may survive for months or even years, the proportion of infective eggs decreases rapidly after 3–6 months (Ilsøe et al., 1990).

The egg dispersal mechanisms discussed above are responsible for indirect ingestion of parasite eggs which will be in relatively low numbers, leading to light infection or no infection at all, as suggested by transmission/infection scenarios 3 and 4 above.

2.6. Indirect human to pig transmission: contaminated feed and water from poor hand hygiene

The key to perpetuation of transmission of *T. solium* is the contact between the pigs and the human faecal matter containing infective eggs (Okello and Thomas, 2017). Poor personal/hand hygiene of tapeworm carriers may lead to transmission to pigs through contamination of food or water, even in the absence of any dispersal mechanism. Poor hand hygiene has been associated with a greater risk of exposure to porcine cysticercosis (Vora et al., 2008). A survey in Mbeya Rural and Mbozi districts speculated that majority of farmers did not wash their hands after toilet use, and before feeding pigs (Kabululu et al., 2020b). In Uganda, the situation had been reported before whereby just over half (54.6%) of interviewed farmers had clean water near the latrines for washing hands (Kungu et al., 2017). In addition, even when they do wash their hands after latrine use, only a few use soap, as it was observed by Kungu et al. (2017). In such situations, transmission may occur when farmers engage in preparation and/or providing feed or water to pigs. In a study by Braae et al. (2015) in Mbeya Rural and Mbozi districts, infection in pigs was associated with feeding them with potato peels. Among the points of contamination which were speculated was handling of the potatoes by a tapeworm carrier such as when peeling them. In an earlier study in Mbozi District, for example, it was indicated that it was a common practice for multiple people to use same water in which to wash their hands by dipping, instead of using running water. This was associated with higher positivity of human cysticercosis (Mwanjali et al., 2013). It would not be surprising if such water is provided to pigs, exposing them to *T. solium* eggs.

Poor hand hygiene, especially of tapeworm carriers, will lead to indirect ingestion of parasite eggs which will be in low numbers, resulting to light infections, or no infection at all.

2.7. Pig to pig transmission: secondary infection to pigs

Gonzalez et al. (2006) showed that pigs infected orally with *T. solium* proglottids containing infective eggs were able to infect naïve pen mates. The pigs which were secondarily infected carried much lower cysticerci intensities than did primarily infected pigs. Although the authors did not exclude the possibility that transmission did not occur due to contamination of the mouth/snout of the animals receiving the primary infection, if infective eggs did pass in the faeces, this type of transmission could partly explain the aggregated nature of porcine cysticercosis. Further, this route of transmission raises the possibility that a free roaming pig infected through coprophagia while freely roaming could bring the infection to the pen and infect pen mates.

2.8. Pig to human transmission: 'Hidden' risk of light cysticerci intensities

Pigs infected with viable cysticerci pose a public health risk to humans, as consumption of undercooked pork from an infected pig is the major risk factor for taeniasis. On quantitative terms, it seems safe to assume that pigs with heavy cysticerci loads raise greater public health concern as they contribute immensely to the number of infected pork meals consumed in endemic areas (Braae et al., 2019; Santamaría et al., 2002; Singh et al., 2018; Thomas et al., 2017). In addition, heavily infected pigs are normally not taken to official slaughter slabs, as they are more likely to be detected through tongue examination by pig traders/farmers. Hence, such pigs are often sold/slaughtered in a clandestine manner, circumventing official inspection and hence pose a public health risk. Equally, it is argued here that pigs with light infections could pose as big public health risk as pigs with heavy infections. This is because, firstly, a heavily infected pig/carcase can easily be detected ante mortem through lingual examination and upon slaughter. Secondly, the aggregated nature of porcine cysticercosis implies that the associated risk is aggregated among a minority of the infected pigs. It is supposed that a visible and aggregated risk could probably be easier to control than a less visible, dispersed risk associated with lighter infections. It has been reported in Mbeya Rural and Mbozi districts that 61% of the interviewed farmers who had seen cysticerci in pork did not know that consumption of the infected pork could lead to taeniasis (Kabululu et al., 2020b). This could indicate that the people would consume infected pork anyway. However, it is claimed that there is a possibility that people might be deterred from consuming grossly infected meat for aesthetic reasons, regardless of whether they are aware of the health risk involved or not. It is also argued that even when they decide to consume the meat, the 'measly' appearance of the meat will prompt an extra effort to thoroughly cook the meat by sheer 'fear of the unknown', hence reducing the risk associated with consuming the meat.

On the other hand, lightly infected pigs are likely to be missed by lingual examination and routine meat inspection. Lingual examination has been reported to have a sensitivity as low as 16% but increases to about 70% depending on cysticerci intensity (Dorny et al., 2004; Gonzalez et al., 1990; Phiri et al., 2006; Sciutto et al., 1998b). Lightowlers et al. (2015) reported that 6% of cysticerci in slaughtered pigs were located on the tongue. Upon being missed by lingual examination, infected pigs will progress to slaughter and subjected to routine meat inspection. Although routine meat inspection has been reported to have a better sensitivity compared to lingual examination, its sensitivity depends on infection intensity, number of incisions made and the skill of the inspector (Chembensofu et al., 2017; Dorny et al., 2004; Sciutto et al., 1998a). Employing available pork inspection guidelines in Tanzania, Boa et al. (2002), using 24 naturally infected finished pigs, found that only 10.6% of all cysticerci in the infected pigs would be located at inspected/sliced sites. It is important to note here that pigs in this study by Boa and others were pre-selected based on tongue examination, hence they were not really representing the general pig populations in the area. Hence it can be speculated that if randomly selected pigs were used, a lower proportion (<10.6%) of cysticerci would be located at the inspected/sliced sites.

Moreover, a recent paper has reported the use of 'street-level-diplomacy' by the meat inspectors, among other frontline actors involved in meat safety in northern Tanzania (Hrynick et al., 2019). Being cognizant to the socio-economic context in which they worked and lived, the meat inspectors were reported to be hesitant to act punitively unless absolutely necessary. This kind of 'diplomacy' could also be in use in the pork value chains in the country, and probably elsewhere, leading to entry of infected meat into the food chain. The consumers will unsuspiciously consume the meat unaware of the underlying risk, and no extra care will be taken to ensure the meat is well cooked before being consumed. In addition, although *T. solium* infections have been reported to be occurring in clusters, lighter infections entail a possibility of transmission to distant urban areas. When missed upon tongue inspection by pig traders who usually inspect pigs before buying them, the pigs may get transported to distant urban areas. It has been reported that slaughter pigs from Mbeya Rural and Mbozi districts are sometimes transported to distant areas up to 900 km away (Kabululu et al., 2020b) and this could lead to transmission of the disease far and beyond areas in which the parasite is known to be endemic.

2.9. Control options: need for an increased focus on indirect routes of transmission

In this paper, an argument has been put forward that light *T. solium* cysticerci intensities in pigs could pose a high public health risk. We therefore advocate for more attention to indirect routes of transmission which most likely result to moderate/light infection intensities.

As transmission of *T. solium* to pigs has been largely associated with pig coprophagic behaviour, control, therefore, seem feasible by corralling pigs and hence preventing pig free roaming. However, as studies have indicated the possibility of in-pen transmission through contaminated feeds and water (Braae et al., 2015; Komba et al., 2013), confining pigs alone would not be enough as a control measure. The importance of providing confined pigs with clean and safe feed and water should be emphasized. On the other hand, while preventing indiscriminate defaecation by promoting and enforcing proper use of latrines is expected to prevent pig access to human faeces, 'open 'latrines still present a risk hence should be discouraged. Moreover, personal hygiene, particularly hand hygiene of the people in the communities should be improved so as to prevent transmission to pigs, especially from people engaged with handling and providing pigs with feed and water. In a survey involving school children in India, no cases of *Taenia* infections were found among children who practiced washing hands with soap, which showed that proper hand hygiene is an effective method of interrupting transmission of *T. solium* to pigs (Sah et al., 2012).

As carcases with a few cysticerci are likely to pass undetected during routine meat inspection, and it is not practical to increase the number of incisions made during pork inspection, more education needs to be provided regarding thorough cooking of pork. A recent study which assessed the effect of temperature and time on the viability of *T. solium* cysticerci advised that to be safe for consumption, pork pieces should be boiled for at least 10 min, before being fried or grilled (Møller et al., 2020). Lastly, although improvement in pig husbandry practices and communities' sanitation and hygiene standards will interrupt transmission of *T. solium*, this seems to be far from realization in many endemic areas. A pig vaccine - TSOL18 - for prevention of *T. solium* infection in pigs and an anthelminthic – oxfendazole - for killing cysticerci already established in pigs' tissues have been trialed for effectiveness and have shown promising results (Assana et al., 2010; Kabululu et al., 2020a; Nsadha et al., 2021; Poudel et al., 2019a).

3. Conclusion

In conclusion, this paper has reviewed several intrinsic and extrinsic factors which possibly influence aggregation of *T. solium* cysticerci in pigs. While heavy infections are associated with direct ingestion of infective eggs released by tapeworm carriers, lighter infections are mostly a result of indirect routes of transmission. While we acknowledge the risk associated with heavy infections, we argue that light infections present a 'hidden' risk and a particular public health concern because they are likely to be missed both ante- and post mortem hence they can easily enter the food chain and present a public health risk. For more effective and sustainable control strategies, we advocate for more attention to indirect routes of transmission. Pigs should be corralled and provided with clean and safe feed and water. In addition, emphasis should be put on proper use of latrines, good personal hygiene and thorough cooking of pork.

Declaration of Competing Interest

Uffe C. Braae is currently employed by Novo Nordisk A/S. There is no conflict of interest to declare for other authors

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