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Conlan, J.V., Vongxay, K., Fenwick, S., Blacksell, S.D. and Thompson, R.C.A. (2009) Does interspecific competition have a moderating effect on *Taenia solium* transmission dynamics in Southeast Asia. *Trends in Parasitology*, 25 (9), pp. 398-403.

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Does interspecific competition have a moderating effect on *Taenia solium* transmission dynamics in Southeast Asia?

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Abstract

It is well understood that sociocultural practices strongly influence *Taenia solium* transmission; however, the extent to which interspecific parasite competition moderates *Taenia* transmission has yet to be determined. This is certainly the case in Southeast Asia where *T. solium* faces competition in

both the definitive host (people) and the intermediate host (pigs). In people, adult worms of *T. solium*, *T. saginata* and *T. asiatica* compete through density-dependent crowding mechanisms. In pigs, metacestodes of *T. solium*, *T. hydatigena* and *T. asiatica* compete through density-dependent immune-mediated interactions. Here, we describe the biological and epidemiological implications of *Taenia* competition and propose that interspecific competition has a moderating effect on the transmission dynamics of *T. solium* in the region. Furthermore, we argue that this competitive ecological scenario should be considered in future research and surveillance activities examining *T. solium* cysticercosis and taeniasis in Southeast Asia.

***Taenia* in Southeast Asia**

Cysticercosis and taeniasis caused by the zoonotic tapeworm *Taenia solium* accounts for significant morbidity in many regions of the world, particularly in less developed countries where poor hygiene practices are common and sanitation is limited [1-3]. The *T. solium* taeniasis and cysticercosis infection complex is wholly dependent on a two-host life cycle involving pigs and humans [4]. Humans are the only natural definitive host acquiring the adult tapeworm (taeniasis) following ingestion of pork containing the larval stage of the parasite (cysticerci). Tapeworm carriers act as a source of infection for pigs and humans who become infected with cysticerci after ingesting eggs shed in faeces [4].

In Southeast Asia, socioeconomic conditions and meat consumption habits predispose many of its inhabitants to *T. solium* taeniasis and cysticercosis [5-8]. However, the natural environment in the form of parasite competition might lend a helping hand in limiting the abundance and impact of *T. solium*. Humans are the definitive host for three *Taenia* species - *T. solium*, *T. saginata* and *T. asiatica* [8-10] - and pigs are the known intermediate host for three *Taenia* species - *T. solium*, *T.*

asiatica and *T. hydatigena* [8, 11]. Canines are the definitive host for *T. hydatigena* and bovines are the intermediate host for *T. saginata* [12] (Figure 1).

Taeniasis and cysticercosis in Asia has been the subject of recent reviews [1,5,8,13,14] with a focus on *T. solium* and *T. asiatica* [13,14]. But for the most part, accurate data on *T. solium* and other *Taenia* species are lacking (cited by Ref. [15]). This is especially true for some of the poorest countries in the region including Laos, Cambodia [7,16] and Myanmar. *Taenia hydatigena*, typically associated with ovines, rarely rates a mention with regards to pig infection in Southeast Asia, and then most often merely as a nuisance in immunological test specificity [17,18]. This is despite the fact that *T. hydatigena* is often observed in a substantial proportion of pigs in countries such as Vietnam [8,11].

To our knowledge, the ecological and competitive interactions of *T. solium* with other related species have not been investigated. This article will describe the biological factors related to *Taenia* ecology in the definitive and intermediate hosts before outlining the implications for parasite transmission. These arguments subsequently lead us to the hypothesis that interspecific competition has a moderating effect on *T. solium* transmission dynamics in the Southeast Asian region. Furthermore we argue that substantial knowledge gaps exist in our understanding of these competitive interactions and greater research emphasis is required to correct this deficit.

The definitive host

Biotic potential

The biotic potential of a taeniid parasite influences the extent to which the environment is contaminated by infective eggs, which in turn influences the dynamics of transmission to the

intermediate host [19]. It has been defined as the potential number of viable metacestodes produced per infected individual definitive host per day, and is a product of the mean number of eggs shed per infected definitive host per day and the proportion of eggs that survive as viable metacestodes in the intermediate host [20] (Table 1).

Crowding and competition in the definitive host

The ‘crowding effect’ is a well-established concept in cestode ecology and refers to inter- and intraspecific competition between adult worms in the definitive host [21-24]. Cestode crowding, regardless of the mechanism involved, leads to a reduction in parasite fitness and subsequently a reduction in parasite size and egg output [23,24]. For the large *Taenia* tapeworms infecting humans, multiple worm burdens in a single host are certainly not uncommon [6,25] and a dual infection of *T. asiatica* and *T. solium* has recently been reported in Thailand [6]. But what is the effect on the worms involved? Tesfa-Yohannes [25] reported an approximate 25% decrease in the mean number of segments per worm for persons with two *T. saginata* worms compared to persons with a single worm infection. If we use *T. hydatigena* as a guide [26], then we can argue that the reduced number of proglottids observed by Tesfa-Yohannes [25] resulted from a reduction in the number of pre-gravid and gravid proglottids. The number of immature and mature proglottids per worm for *T. hydatigena* does not vary with increased worm burden, rather it is the number of pre-gravid and gravid proglottids per worm that decreases [26] leading to a reduction in egg output. This is further supported by Allan and colleagues [27] who report a taeniasis case involving at least seven *T. solium* worms that were all sexually immature. Thus, humans can happily host more than one *Taenia* worm, whose fitness decreases with increasing numbers.

What, therefore, is the effect on biotic potential? In a single *Taenia* species superinfection, intraspecific competition might have limited impact on biotic potential as the reduced egg output per

worm will be compensated for by an increase in worm density. But this reasoning cannot be applied to competition in the human host involving more than one *Taenia* species. The reduced egg output per worm will not be compensated for by an increased worm density leading, in turn, to a reduced egg output per species and a reduction in biotic potential. In an environment where three species of *Taenia* sympatrically coexist, crowding and competition in the human definitive host would be expected to moderate transmission to the intermediate host. As an example, if a *T. solium* metacestode were able to overcome the competition barriers and establish as an adult in the presence of *T. saginata* or *T. asiatica*, the number of eggs produced would be predicted to be fewer than for a single worm infection. A subsequent reduction in the number of viable eggs contaminating the environment would moderate transmission to susceptible pigs. On the other hand, if the person were already infected with a fully mature *T. saginata* worm, it is unlikely that *T. solium* would establish an infection. This again moderates the transmission of *T. solium*. In our opinion, the nature of this competition and the effects on transmission dynamics has not been adequately investigated.

The intermediate host

Immunity

Immunity in the intermediate host is an important determinant of *Taenia* transmission dynamics and requires some discussion to understand its complexity and how it acts to moderate infection and superinfection. Acquired immunity to *T. solium* in pigs can be elicited by ingestion of eggs [28-31] or artificially induced by vaccination (reviewed by Ref. [32]). Similar to *T. hydatigena* and *T. ovis* [33], acquired immunity to *T. solium* and other taeniid cestodes occurs in at least two distinct phases - pre-encystment and post-encystment [12]. Pre-encystment immunity to *T. hydatigena* in sheep begins to wane from between three to five months and post-encystment immunity wanes from 12 months (cited by Ref. [33]). Similar data are not available for *T. hydatigena* in pigs. Post-encystment immunity to *T. solium* in pigs begins to wane from between five and nine months after primary infection and pigs become susceptible to re-infection while still harbouring viable cysticerci [30].

Recent experimental research indicates that age at primary egg exposure and innate immunity might be important determinants of cysticercus survival and longevity [28]. Deckers and colleagues [28] found that naive pigs infected with a single gravid proglottid at one month of age and euthanised three months post-infection harboured mostly viable cysts (98.1% viable), whereas five-month-old pigs infected in the same manner and euthanised three months post-infection harboured mostly degenerated cysts (1.5% viable) [28]. An intermediate infection outcome was observed in pigs infected at three months of age (44.9% viable) [28]. These results do appear to be consistent with the reduced survival and longevity of *T. saginata* cysticerci in older animals (cited by Ref. [34]), but the role of innate immunity in cysticercus survival remains to be demonstrated in the field.

In addition to acquired and innate immunity, protection can be transferred from a sow to her offspring via colostrum [35,36]. Maternal antibodies to the gp50 protein of *T. solium* can persist for longer than 20 weeks but the majority of maternal antibodies begin to wane from eight to 14 weeks of age [35,36] suggesting a level of protection against infection in young pigs. Passive immunity has been characterised for *T. ovis* and *T. hydatigena* in sheep [37] but data relating to passive immunity against *T. hydatigena* and *T. asiatica* in pigs are limited.

Interspecies immune-mediated interactions and competition

Cross-immunity between *Taenia* species has been well documented and characterized for the ovine cysticerci of *T. ovis* and *T. hydatigena* [33], and is capable of significantly modifying the transmission dynamics of competing species [33]. Sheep that had already been exposed to *T. hydatigena* eggs were able to reject *T. ovis* eggs when given together with *T. hydatigena* eggs (cited by Ref. [33]). Similarly, sheep immunised with *T. hydatigena* eggs were better able to evade establishment of viable *T. ovis* larvae than were sheep vaccinated with *T. ovis* to evade establishment of viable *T.*

hydatigena larvae (cited by Ref. [33]). Similar data are not available for reciprocal immune-mediated competition for the *Taenia* species infecting pigs in Asia. However, cross-reactivity exists between immunogenic antigens of heterologous *Taenia* species (cited by Ref. [32]) [38] and suggests that reciprocal immunity and immune-mediated competition does exist between *T. solium*, *T. hydatigena* and *T. asiatica*.

A combination of the differing immune responses and interspecific immunologic cross-reactivity results in a moderating effect on cysticercus density and viability in pigs. Acquired immunity is conferred by exposure to eggs rather than the presence of dead or viable cysts, so in a strong infection pressure environment, there is a relatively short window of opportunity for viable cysts to establish in the intermediate host [20]. Where three species of *Taenia* sympatrically co-exist in the pig population, exposure to eggs of say *T. hydatigena* might prevent or limit the establishment of viable cysts of *T. solium* or *T. asiatica*. In a low infection pressure environment, waning of pre- and post-encystment immunity might lead to new infections establishing upon re-exposure and greater cyst burdens in older animals [20]. Waning of immunity to one species might also provide an opportunity for viable cysticerci of a different *Taenia* species to establish in the same pig. This has been observed in Zambia where co-infections of *T. hydatigena* and *T. solium* have been documented [39]. Data on dual infections of *T. hydatigena*, *T. solium* and *T. asiatica* in Southeast Asia are scarce.

In an environment such as Southeast Asia, where the opportunity exists for three *Taenia* species to compete in the intermediate host, the infection pressure of all competing species should be considered when assessing transmission dynamics. To the best of our knowledge, no studies have been undertaken that examine *T. hydatigena* abundance in dogs concurrently with studies in pigs and humans.

General epidemiological considerations

Limitations of surveillance in the intermediate host

Immunodiagnostic methods for taeniid cestodes have recently been reviewed [17,40]. With respect to field surveillance for *T. solium*, antibody detection by electroimmunotransfer blot (EITB) [41] or enzyme-linked immunosorbent assay (ELISA) (reviewed in Ref. [17,40]) is difficult to analyse in endemic areas owing to the persistence of maternal antibody in piglets up to four to seven months of age [35]. In addition, the EITB is prohibitively expensive in many developing countries (cited by Ref. [17]) and antibody ELISA has only moderate sensitivity [39]. The antigen ELISA [42] has high sensitivity but lacks the ability to distinguish between different species of *Taenia* cysts in pigs [17]; however, new diagnostic technologies are under development and might allow species specific detection [18]. Surveillance in abattoirs and slaughter slabs also presents diagnostic problems. Meat inspection is highly specific but sensitivity is very low [39] and varies according to cyst density and inspector competence. A combination of all these factors results in survey data from pigs that are difficult to interpret and age-intensity profiles that are almost impossible to determine.

Basic reproductive rate

For macroparasites, the basic reproductive rate (R_0) is defined as the expected number of mature offspring that one adult parasite will produce in its lifetime [43,44] and by definition it is the rate that would be achieved in the absence of density-dependent constraints [44,45]. This rate is an important concept in epidemiology and determines the transmission dynamics and environmental stability of the parasite [19,20]. For taeniids, if R_0 is less than one, the parasite is unable to maintain itself and is predicted to become extinct with time [45]; an R_0 equal to or slightly greater than one is indicative of an endemic steady state with little regulation from density-dependent constraints [19,45]. A value of R_0 much greater than one indicates there is some regulation by density-dependent constraints such as herd immunity in the intermediate host [19,45]. The calculation and interpretation of R_0 for taeniids

is, however, complicated by the assumption of no density-dependent constraints on the parasite life cycle [19]. Even so, R_0 values have been estimated for *Echinococcus* and the ovine cysticerci of *T. ovis* and *T. hydatigena* using age-intensity and age-prevalence data [46-49]. It stands to reason however, that in an environment where age-intensity and age-prevalence profiles in the intermediate host cannot be reliably measured, the application of R_0 in assessing transmission dynamics is limited. That few, if any, researchers have attempted to quantify R_0 for *T. solium* in Southeast Asia is a testament to this reality and discussions will remain essentially theoretical until improved diagnostic technologies are widely available.

Existing models and interspecific competition

Mathematical models have been developed for *T. solium* [50] and other taeniid cestodes [47-49] to describe transmission dynamics. Kyvsgaard *et al.* [50] developed a model that described transmission between infected and susceptible categories depending on the probability of transmission from each random contact made during a pre-specified time increment. The model was useful for predicting outcomes of control interventions [50], but the oversimplification of *Taenia* immunity makes it inappropriate for application in an environment where interspecific competition exists in the intermediate and definitive hosts.

Roberts *et al.* [48] developed a model for the ovine cysticerci of *T. hydatigena* and *T. ovis* that described the variation of prevalence with the age of the intermediate host, taking into account the effects of acquired and lost immunity. The model for individual parasites was adapted to model the effects of interspecific competition [48]. The model demonstrated that reducing R_{0-1} for one species with little change to R_{0-2} of a second species results in a reduction in the population of species '1' and increases the population of species '2' [48]. Field data from New Zealand support the validity of this competition model [48].

The competition model described by Roberts *et al.* [48] has important implications for the Southeast Asian region. The model and supporting field observations demonstrate that transmission of one tapeworm can moderate the transmission of a closely related second tapeworm. We might predict that a reduction in R_0 *T. hydatigena* and little change in R_0 *T. solium* and R_0 *T. asiatica* could, in theory at least, lead to a decrease in *T. hydatigena* population and an increase in *T. solium* and *T. asiatica* population. But as we have seen in the preceding discussion, it is difficult to accurately model transmission dynamics and estimate R_0 . This should not be seen as a deterrent, rather it should be seen as a challenge to gather the necessary information to understand the ecology of these competing worms.

Concluding remarks and future perspectives

Environmental and socio-cultural factors strongly influence *Taenia* transmission, but interspecific competition also has an important role in regulating transmission. In our view, these transmission-regulating mechanisms do not operate independently of one another, but rather are complementary. That is to say, socio-cultural practice might give one *Taenia* species a competitive advantage. An example of this would be a preference for eating raw beef as opposed to raw pork, potentially giving *T. saginata* a competitive advantage in the definitive host. This simple example highlights the intricate link between human behaviour and parasite ecology. Although much is already known about the impact of socio-cultural practice on *Taenia* transmission, our knowledge of interspecific immune-mediated competition in pigs is lacking and the impacts of competition in the definitive host are largely unknown. Fundamental studies are needed to understand these interactions from an epidemiological and ecological perspective (Box 1). With this new knowledge, we will have a greater understanding of the implications for *T. solium* control.

Box 1. Research needs for *Taenia* in Southeast Asia

Immunological

- Development of rapid, sensitive and specific point-of-care tests for human taeniasis that are capable of differentiating the three related species *T. solium*, *T. saginata* and *T. asiatica*.
- Development of sensitive and specific tests for the detection of viable *Taenia* infections of pigs that are able to differentiate and semi-quantify intensity of infection of *T. solium*, *T. hydatigena* and *T. asiatica*.
- Development of tests capable of identifying pigs with immunity to the pre-encystment phase of infection.

Epidemiological and ecological

- Development of a comprehensive understanding of the epidemiological and ecological parameters influencing *Taenia* transmission dynamics, including:
 - i. Effects of interspecific crowding in the definitive host on egg production and biotic potential.
 - ii. Infection pressure of *T. solium* and *T. asiatica* from human tapeworm carriers.
 - iii. Infection pressure of *T. hydatigena* from dogs.
 - iv. Age-intensity profiles of the three *Taenia* species infecting pigs and *T. saginata* in cattle and buffalo.
 - v. Regional approaches to understanding the socioecological risk factors for taeniasis and cysticercosis.
 - vi. Regional approach to understanding the pig and pork trade networks and associated risks.
- Characterise passive and acquired immunity of pigs to *T. hydatigena* and *T. asiatica*.
- Investigate the immunological interactions of the three *Taenia* species infecting pigs.
- Develop a regionally focused ecological model of *T. solium* cysticercosis and taeniasis.

Prevention and control

- Regional assessment of the burden of disease resulting from human neurocysticercosis.
- Regional assessment of the socioeconomic impact of *T. solium* cysticercosis in pigs.
- Develop, implement and assess effectiveness of control programs that take an ecological perspective.

Acknowledgements

This research was supported by an Australian Centre for International Agricultural Research (ACIAR) grant and a Murdoch University Research Studentship (MURS) award.

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Figure 1. Life cycle of *Taenia* tapeworms in the context of parasite competition in Southeast Asia. Humans become infected with *T. solium* or *T. asiatica* adult tapeworms after ingesting cysticerci in uncooked pork or pig visceral organs, respectively, and become infected with *T. saginata* adult worms after ingesting cysticerci in uncooked beef. Dogs become infected with *T. hydatigena* adult worms after ingesting cysticerci in uncooked pig visceral organs. *T. saginata* and *T. solium* are musculotropic whereas *T. asiatica* and *T. hydatigena* are viscerotropic. The solid black line within grey shading indicates death of the adult tapeworm; with no lasting immunity, the host becomes susceptible. Pigs are coprophagic and become infected with cysticerci of *T. hydatigena* after ingesting eggs shed in the faeces of infected dogs. Pigs become infected with cysticerci of *T. asiatica* and *T. solium* after ingesting eggs shed in the faeces of infected humans. Cattle and buffalo are not coprophagic and become infected with cysticerci of *T. saginata* after ingesting eggs on pasture or feed contaminated with the faeces of infected humans. The dashed line indicates cysticercus death and a waning of host immunity to susceptible animal status. Humans can become infected with cysticerci of *T. solium* after ingesting eggs shed in the faeces of tapeworm carriers. However, humans infected with *T. solium* cysticerci are dead-end hosts and play no role in transmission or maintenance of the life cycle.

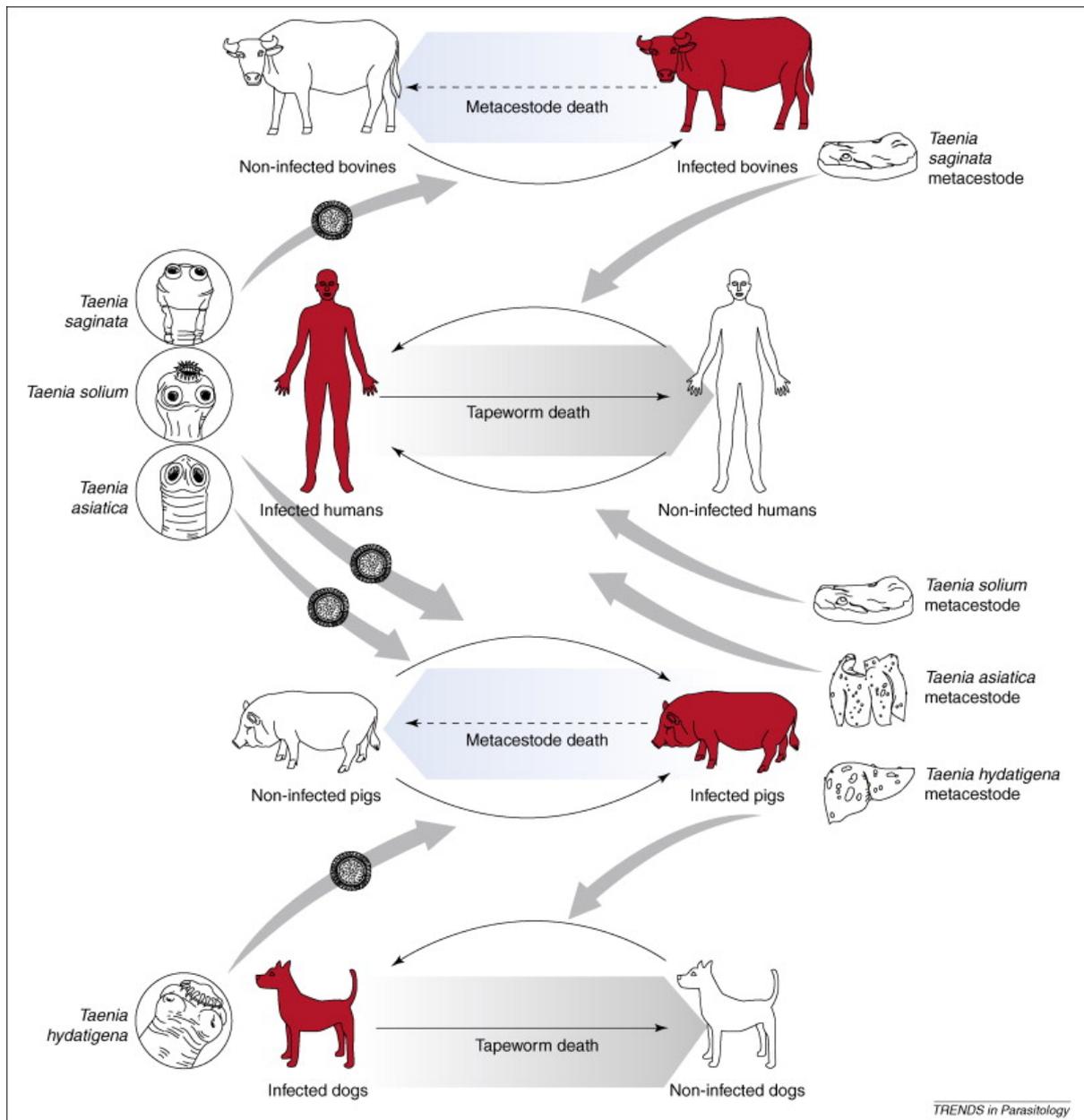


Table 1. Biological parameters influencing the biotic potential of *T. solium*, *T. asiatica*, *T. hydatigena* and *T. saginata*

	<i>T. solium</i>	<i>T. asiatica</i>	<i>T. hydatigena</i>	<i>T. saginata</i>
Prepatent period in definitive host (months)	2	2-6	7-11	3
Number of eggs per proglottid	30,000-60,000	- ^a	30,000-50,000	50,000-100,000
Number of proglottids shed per day	4-5	4-5	1-5	3-10
Usual number of worms per infected definitive host	1	1	1-4	1
Duration of infection in the definitive host (years)	1-5 ^b	- ^a	0.5-1	3-5
Time taken for cysts to become viable (months)	2-3	4-5	3 ^c	2-3
Refs	[4,27,50,51]	[6,52-54]	[20,33,55]	[6,51]

^a not known.

^b In years, but estimated to be approximately 12 months (cited by Ref. [50]).

^c Intermediate host in this case refers to sheep [20], not pigs.