Potentially Zoonotic Helminthiases of Murid Rodents from the Indo-Chinese Peninsula: Impact of Habitat and the Risk of Human Infection

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Abstract

In this study, we report the potential rodent-borne zoonotic helminths in wild-caught murid rodents from four categorized habitats—forest, nonflooded land, irrigated land, and human settlement in seven localities of Thailand, Cambodia, and Lao PDR. Out of 2478 rodent samples, 735 (29.7%) were infected by at least one of the following zoonotic helminth species: *Echinostoma malayanum*, *Echinostoma ilocanum*, *Plagiorchis muris*, *Raillietina* spp., *Hymenolepis diminuta*, *Hymenolepis nana*, *Cyclodontostomum purivisi*, and *Moniliformis moniliformis*. *Raillietina* spp. showed the highest prevalence (13.8%), followed by *H. diminuta* (8.6%), *H. nana* (6.7%), and *C. purvisi* (1.0%). Habitat affected the intensity of helminth infection in murid rodent hosts. Specific habitats favoring each zoonotic helminth species are discussed in relation to the risk of human infection. Season and host maturity influenced intensity of total zoonotic helminths, but there was no influence of host gender. However, in terms of individual helminth species, female rodents were more infected by *E. malayanum, E. ilocanum*, and *C. purvisi* than males. Among the rodent species, *Rattus tanezumi* seems to play the most important role as a reservoir by hosting seven zoonotic heminth species. This rat is ubiquitously found in all types of the habitats, suggesting that it can act as an important bridge species, carrying parasites across different habitats.

Key Words: Rodent—Zoonosis—Helminth—Habitat—Thailand—Cambodia—Lao PDR.

Introduction

RODENTS NOT ONLY ACT as important reservoirs of microparasites causing substantial human diseases, such as hantaviruses, cowpox, hepatitis E, leptospirosis, plague, murine typhus, toxoplasmosis, bartonellosis, and others, but they also harbor a number of zoonotic macroparasites, *e.g.*, helminthiases (Graczyk and Fried 1998, Spratt 2005, Meerburg et al. 2009, Herbreteau et al. 2012, Bordes et al. 2013).

Helminthiases are considered as neglected diseases, with low public health importance because they produce infections that have low levels of severity in healthy people. Nevertheless, in immunocompromised and immunosuppressive cases (*i.e.*, human immunodeficiency virus [HIV], cancer, organ transplant, radiation sickness, or patients under pharmacological treatment for autoimmune problems, allergy,

and inflammatory disorder), helminthiases may cause chronic infection, hyperinfection syndrome, and unusual manifestations in vital organs (Wolday et al. 2002, Delobel et al. 2004, Keiser and Nutman 2004, Syafinaz et al. 2011). In addition, helminth infection in school-aged children significantly impairs physical, nutritional, cognitive, and intellectual development (World Health Organization 1987). Moreover, some zoonotic helminthiases are recognized as important public health concerns, such as echinococcosis, taeniasis, trichinosis, schistosomiasis, filariasis, and opisthorchiasis. Although, these diseases may have less impact compared to the high mortality diseases such as cancer, malaria, tuberculosis, or acquired immunodeficiency syndrome (AIDS), they influence the world population economically and medically.

With respect to the possible role of wild rodents as reservoirs of zoonotic helminthiasis, such studies have been quite

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limited to date. Potential helminth and rodent reservoir species, as well as the impact of different habitats on the human–rodent–helminth interaction, need to be investigated to better understand their epidemiology and surveillance.

This study focused on rodent-borne helminthiasis of the Indo-Chinese Peninsula countries and aimed to: (1) Reveal potential zoonotic helminth species and their rodent reservoir hosts in this region and (2) analyze the likely habitats of such helminths to evaluate the risk of human contact with these parasites.

Materials and Methods

Rodent samples

During the period 2008 to 2012, rodents were collected from 11 sites across the three countries on the Indochinese Peninsula (Fig. 1): Seven sites in Thailand (Buriram, Chiangrai, Kalasin, Kanchanaburi, Loei, Nan, and Prachuabkirikhan), two in Lao PDR (Luang Prabang and Champasak), and two in Cambodia (Sihanoukville and Mondolkiri). In each trapping site, a 12-day trapping procedure with 100 traps per day (1200 trapping pressure per site) were set within the area of approximately $10 \times 10\,\mathrm{km}^2$. Four categorized habitats were selected (applying equal trapping pressure) with regard

FIG. 1. Distribution of rodent sampling localities on Indo-Chinese Peninsula: Thailand (*Chi*, Chiangrai; *Na*, Nan; *Lo*, Loei; *Kal*, Kalasin; *Bu*, Buriram; *Kan*, Kanchanaburi; *Pra*, Prachuabkirikhan), Lao PDR (*Lua*, Luang Prabang; *Cha*, Champasak), and Cambodia (*Mo*, Mondolkiri; *Sih*, Sihanoukville).

to human land use or human disturbed habitats, from low to high levels of disturbance: (1) Forest (primary, secondary, or community forests), (2) upland (nonflooded agricultural lands, fields, or fallows), (3) lowland (irrigated cultivation, *e.g.*, rice fields), and (4) human settlements (houses, villages, or cities). Rodent trapping was set twice on each site in relation to the dry (November to April) and wet season (May to October), except for the sites of Chiangrai, Kalasin, Kanchanaburi, and Prachuabkirikhan, for which a single seasonal trapping survey was performed.

The captured animals were euthanized and identified morphologically in the field using rodent identification keys (Marshall 1988, Aplin 2003). For problematic or cryptic species, molecular barcoding identification was performed using previously defined, specific primers for the *COI* gene (www.ceropath.org/barcoding_tool/rodentsea). The gastrointestinal tracts were isolated and preserved individually in 70% alcohol for further helminthological examination.

Animal handling and procedures of specimen collection followed an international standard (American Veterinary Medical Association Council on Research) and the rodent protocols described by Herbreteau et al. (2011).

Potential zoonotic helminth samples

Gastrointestinal tracts were dissected under a stereomicroscope. Worms were isolated and identified on the basis of their morphology following taxonomic identification keys (Yamaguti 1958, Schmidt 1986, Anderson 2000). To obtain quantitative data, each helminth species from individual rodents was counted to determine the infection intensity.

Among overall helminth species, the potential zoonotic species were inferred by searching from previous human case reports and relevant research publications (Table 1). The present study focuses only on the potential zoonotic helminth species, as overall helminth diversity found in these rodents has been reported elsewhere (Chaisiri et al. 2012, Pakdeenarong et al. 2014).

Statistical analysis

Two main descriptors used to quantify parasite number and analyze our data were zoonotic helminth intensity and total zoonotic helminth intensity, where zoonotic helminth intensity is the number of conspecific helminths found in each infected host and total zoonotic helminth intensity is the sum of the number of all zoonotic helminth species found in each infected host. Nonparametric Kruskal–Wallis and multiple pairwise comparison tests were performed to investigate the effects of habitat on zoonotic helminth intensity. In addition, total zoonotic helminth intensities were analyzed as a function of rodent maturity (juvenile and adult), rodent sex, and season (dry and wet) using the nonparametric Mann–Whitney U-test. These tests were performed with SPSS v. 20.0 software (IBM Corp., 2011) applying 95% confidence intervals.

To show the distribution of zoonotic helminth species found in each of the four habitat types, a principal component analysis (PCA) was performed using the package ade4 implemented in R freeware (Team R Core 2010). The PCA was calculated by counting the number of rodents infected by each helminth species across the four categorized habitats. The prevalence, mean abundance, mean intensity, and range

TABLE 1. STUDIES ON RODENT-BORNE GASTROINTESTINAL HELMINTHIASES IN HUMANS
(WITH AN EMPHASIS ON SOUTHEAST ASIA)

Zoonotic helminth	Taxon	Country	References
Echinostoma malayanum	Trematoda	India, Indonesia, Lao PDR, Malaysia, Philippines, Thailand,	Lie and Viric 1963, Bhaibulaya et al. 1964, Hadidjaja and Oemijati, 1969, Radomyos et al. 1998, Maji et al. 1993, Belizario et al. 2007, Chai et al. 2012
Echinostoma ilocanum	Trematoda	Cambodia, Indonesia, Philippines, Thailand,	Hilarrio and Wharton 1917, Carney et al. 1980, Radomyos et al. 1982, Cross et al. 1986, Sohn et al. 2011
Plagiorchis muris[a]	Trematoda	Japan, Korea	Asada et al. 1962, Hong et al. 1996
Hymenolepis diminuta	Cestoda	Worldwide: Argentina, Chile, China, Cuba, Ecuador, Egypt, India, Indonesia, Iran, Italy, Jamaica, Korea, Malaysia, Mexico, Nepal, Panama, Papua New Guinea, Peru, Poland, Rhodesia, Spain, Taiwan, Thailand, United States	Calvo 1951, Castex et al. 1951, Paul and Zaman 1969, Ghadirian and Arfaa 1972, Reyes et al. 1972, Goldsmid 1973, Cutting 1975, Chitchang et al. 1978, Sinniah et al. 1978, Stafford et al. 1980, Kan et al. 1981, Chung et al. 1985, Levi et al. 1987, Cohen 1989, Min 1990, Tena et al. 1998, Marangi et al. 2003, Waloch 2003, Wiwanitkit 2004, Kunwar et al. 2005, Owen 2005, Cordova et al. 2006, El-Shazly et al. 2006, Jacobsen et al. 2007, Watwe and Dardi 2008, Patamia et al. 2010, Alvarez-Fernandez et al. 2012, Rohela et al. 2012
Hymenolepis nana	Cestoda	Worldwide: Cambodia, Honduras, Indonesia, Korea, Lao PDR, Libya, Malaysia, Mexico, Nepal, Papua New Guinea, Peru, Saudi Arabia, Singapore, Taiwan, Thailand, Vietnam	Cheah and Kan 1971, Cross et al. 1976, Chung et al. 1985, Min 1990, Kaminsky 1991, Jongsuksantigul et al. 1992, Sherchand et al. 1996, Toma et al. 1999, Sirivichayakul et al. 2000, El-Sheikh and El-Assouli 2001, Park et al. 2004, Le Hung et al. 2005, Owen 2005, Chhakda et al. 2006, Sithithaworn et al. 2006, Ben-Musa 2007, Chero et al. 2007, Sohn et al. 2011, Syafinaz et al. 2011, Alvarez-Fernandez et al. 2012
Raillietina spp.	Cestoda	China, Costa Rica, French Polynesia, Indonesia, Japan, Thailand	Chandler and Pradatsundarasar 1957, Areekul and Radomyos 1970, Rougier et al. 1981, Brenes et al. 1983, Beaver et al. 1984, Margono 1989
Cyclodontostomum purvisi	Nematoda	Thailand	Bhaibulaya and Indra-ngarm 1975
Moniliformis moniliformis[a]	Acanthocephala	Australia, Iran, Iraq, Nigeria, United States	Moayedi et al. 1971, Al-Rawas et al. 1977, Counselman et al. 1989, Ikeh et al. 1992, Berenji et al. 2007, Salehabadi et al. 2008

[a]Human cases have not been reported in Southeast Asia.

of each zoonotic helminth infection were estimated by Quantitative Parasitology software, v. 3.0 (Rozsa et al. 2000).

Results

Among 18 murid rodent species (2478 individuals), eight potential zoonotic helminths were found in 735 rodents (29.66%). *Raillietina* spp. showed the highest prevalence (13.8%) followed by *Hymenolepis diminuta* (8.6%), *Hymenolepis nana* (6.7%), *Cyclodontostomum purvisi* (1.0%), *Plagiorchis muris* (0.4%), *Echinostoma ilocanum* (0.2%), *Echinostoma malayanum* (0.2%), and *Moniliformis moniliformis* (0.2%).

Rattus tanezumi harbored the highest number of zoonotic helminth species (six), followed by the other rodents, *Bandicota indica, Bandicota savilei, Mus caroli, Mus cervicolor,* *Mus cookii, Rattus exulans*, and *Rattus sakaretensis*, each of these harboring four helminth species (Table 2).

Total zoonotic helminth intensity varied significantly among the four categorized habitats (Kruskal–Wallis test = 48.42, $p < 0.001$) (Fig. 2). In addition, most of the species showed significant differences between habitats, such as *E. ilocanum* (Kruskal–Wallis test = 15.32, $p = 0.002$), *P. muris* (Kruskal–Wallis test = 11.18, $p = 0.011$), *H. diminuta* (Kruskal–Wallis test = 60.21, $p < 0.001$), *H. nana* (Kruskal–Wallis test = 66.15, $p < 0.001$), *C. purvisi* (Kruskal–Wallis test = 14.61, $p = 0.002$), and *M. moniliformis* (Kruskal–Wallis test = 9.43, $p = 0.024$), whereas this was not the case for *E. malayanum* (Kruskal–Wallis test = 2.14, $p = 0.54$) (Fig. 3).

The PCA plot (Fig. 4) shows the associations between the zoonotic helminth species and habitat types, where the first

Table 2. Prevalence (%), Mean Abundance (MA), Mean Intensity (MI), and Range of Potential Rodent–Borne Zoonotic Helminthes in 18 Rodent Species (N=2478) from Thailand, Cambodia, and Lao PDR (see Materials and Methods)

| Rodent species (n)	Helminth species	Prevalence (%)	MA	MI	Range
Bandicota indica (287)	Echinostoma ilocanum	2.1	1.66	79.17	0–293
	Raillieina spp.	43.9	3.02	6.88	0–30
	Hymenolepis diminuta	0.7	0.01	1.00	0–1
	Cyclodontostomum purvisi	0.3	0.01	4.00	0–4
Bandicota savilei (149)	Echinostoma malayanum	1.3	0.07	5.50	0–10
	Raillietina spp.	29.5	0.84	2.84	0–10
	Hymenolepis diminuta	10.7	0.25	2.31	0–10
	Cyclodontostomum purvisi	10.1	1.09	10.87	0–30
Berylmys berdmorei (52)	Raillietina spp.	21.2	0.40	1.91	0–5
	Hymenolepis diminuta	7.7	0.29	3.75	0–10
Berylmys bowersi (37)	Raillietina spp.	2.7	0.03	1.00	0–1
	Hymenolepis diminuta	8.1	0.46	5.67	0–10
Leopoldamys edwardsi (16)	Raillietina spp.	37.5	1.56	4.17	0–10
	Hymenolepis diminuta	37.5	5.19	13.83	0–30
	Cyclodontostomum purvisi	12.5	0.13	1.00	0–1
Maxomys surifer (154)	Raillietina spp.	3.9	0.11	2.83	0–10
	Hymenolepis diminuta	3.2	0.08	2.60	0–4
	Cyclodontostomum purvisi	2.6	0.27	10.25	0–30
Mus caroli (135)	Plagiorchis muris	5.2	0.47	9.14	0–41
	Raillietina spp.	2.2	0.03	1.33	0–2
	Hymenolepis diminuta	0.7	0.01	1.00	0–1
	Hymenolepis nana	12.6	0.21	1.71	0–4
Mus cervicolor (198)	Raillietina spp.	5.1	0.17	3.40	0–10
	Hymenoplepis diminuta	1.0	0.03	3.00	0–4
	Hymenolepis nana	28.8	1.49	5.18	0–30
	Cyclodontostomum purvisi	1.5	0.03	2.00	0–4
Mus cookii (207)	Plagiorchis muris	0.5	<0.01	1.00	0–1
	Raillietina spp.	1.4	0.03	2.33	0–5
	Hymenolepis diminuta	3.4	0.09	2.71	0–10
	Hymenolepis nana	34.8	0.87	2.5	0–30
Mus pahari (5)[a]	Hymenolepis nana	40.0*	0.80	2.00	0–3
Niviventer fulvescens (93)	Raillietina spp.	16.1	0.37	2.27	0–10
	Hymenolepis diminuta	34.4	0.83	2.41	0–10
	Hymenolepis nana	4.3	0.04	1.00	0–1
Rattus andamanensis (6)[a]	Cyclodontostomum purvisi	16.7*	3.33	20.00	0–20
Rattus argentiventer (17)	Hymenolepis diminuta	5.9	0.06	1.00	0–1
Rattus exulans (545)	Raillietina spp.	1.5	0.03	0.38	0–10
	Hymenolepis diminuta	13.0	0.43	3.34	0–18
	Hymenolepis nana	0.4	0.01	1.50	0–2
	Moniliformis moniliformis	0.5	0.01	1.67	0–3
Rattus losea (125)	Echinostoma malayanum	1.6	0.03	2.00	0–3
	Raillietina spp.	16.0	0.50	3.10	0–30
	Hymenolepis diminuta	0.8	0.02	2.00	0–2
	Hymenolepis nana	1.6	0.09	5.50	0–10
Rattus nitidus (14)	Raillietina spp.	7.1	0.14	2.00	0–2
	Hymenolepis diminuta	21.4	0.21	1.00	0–1
Rattus norvegicus (17)	Raillietina spp.	41.2	0.41	1.00	0–1
	Hymenolepis diminuta	23.5	0.24	1.00	0–1
Rattus tanezumi (421)	Echinostoma malayanum	0.2	<0.01	1.00	0–1
	Plagiorchis muris	0.2	<0.01	2.00	0–2
	Raillietina spp.	19.2	0.55	2.84	0–30
	Hymenolepis diminuta	13.3	0.28	2.11	0–30
	Hymenolepis nana	0.2	<0.01	1.00	0–1
	Moniliformis moniliformis	0.3	0.01	3.00	0–3

[a]Host sample size <10.
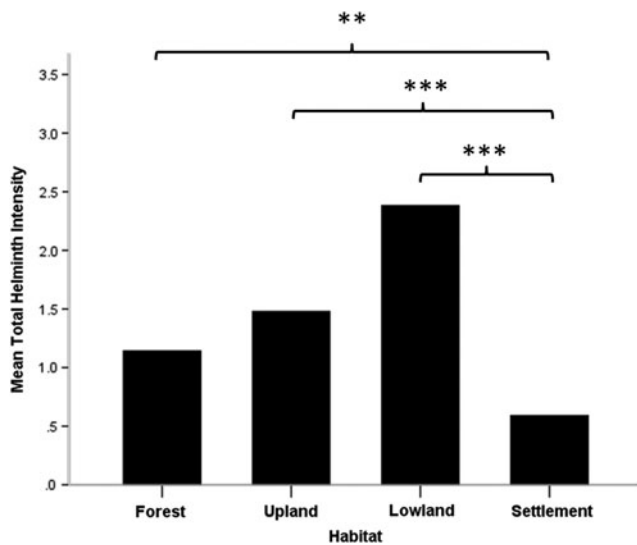
FIG. 2. Analysis of differences in total zoonotic helminth intensity among each habitat with multiple pairwise comparisons after Kruskal–Wallis test. (*) $p < 0.05$, (**) $p < 0.01$, (***) $p < 0.001$.

and second dimensions explain 80% of the total variance. Several helminth species seemed to have specialized habitat preferences: *M. moloniformis* preferred settlements; *E. ilocanum* and *E. malayanum* tended to be found in rain-fed fields; and *P. muris, C. purvisi*, and *H. nana* had a prediction for nonflooded (or dry) lands. *Raillietina* spp. and *H. diminuta* appeared to be more general in habitat preference, as they were found in forests and rain-fed lands, and forest-settlement habitats, respectively.

There was no difference in total zoonotic helminth intensity between male and female rodents (Mann–Whitney test = −0.45, $p = 0.65$), but significant differences of individual helminth intensity were found between rodent genders. Female rodents harbored significantly higher intensity in *E. malayanum* (Mann–Whitney test = 2.079, $p = 0.038$), *E. ilocanum* (Mann–Whitney test = 2.278, $p = 0.023$), and *C. purvisi* (Mann–Whitney test = −2.747, $p = 0.006$), whereas no significantly higher helminth intensity was found in male rodents. Total zoonotic helminth intensity in adult rodents was significantly higher than in juveniles (Mann–Whitney test = −3.13, $p = 0.002$). Also, the seasonal comparison showed that rodents in the wet season harbored significantly higher total zoonotic helminth intensities than the rodents from the dry season (Mann–Whitney test = −4.31, $p < 0.001$).

Discussion

Main rodent-borne zoonotic helminths and their reservoirs in the Indo-Chinese Peninsula

E. malayanum. This fluke is found in small intestine of various animals including humans, rodents, dogs, pigs, and birds (Belizario et al. 2007, Chai et al. 2009). To complete its life cycle, fresh water snails (*e.g.*, *Lymnaea*, *Indoplanorbis*, etc.) and a number of aquatic organisms such as other snails, tadpoles, frogs, and fish act as, respectively, first and second intermediate hosts (Sornmani 1969, Rim 1982). Humans

become infected by ingestion of encysted metacercaria in the second intermediate hosts, which develop into the adult stage producing ulceration to the intestinal mucosa. In cases of heavy infection, necrosis and infiltration of the mucosa potentially occur, leading to diarrhea (Graczyk and Fried 1998). Previously, *E. malayanum* has been reported in *Rattus argentiventer, R. exulans, R. jalorensis, R. mindanensis mindanensis, R. norvegicus, R. rattus*, and *R. rattus diardii* (Joe 1963, Betterton and Lim 1975, Sinniah 1979, Monzon and Kitikoon 1989, Namue and Wongsawad 1997, Salcedo and Glenn 2006). In the present study, three rodent species: *B. savilei* from Thailand (Loei), *R. tanezumi* from Cambodia (Mondolkiri), and *R. sakaretensis* from Lao PDR (Pakse) were found to be infected and potentially may act as a reservoir of *E. malayanum* infection in humans.

E. ilocanum. Similar to *E. malayanum*, *E. ilocanum* is an intestinal parasitic fluke in mammals and birds. The worm has an indirect life cycle with aquatic snails as intermediate hosts: *Gyraulus* and *Hippeutis* are first intermediate hosts, whereas *Pila*, *Viviparous*, *Thiara*, *Planorbis*, and *Lymnaea* act as second intermediate hosts. Humans have been reported as an accidental host by ingestion of metacercaria-infected snails. However, the incidence of *E. ilocanum* infection in humans is quite low, which may be related to the fact that the second intermediate hosts are not consumed by humans (Sirivichayakul et al. 2006). In the present study, *E. ilocanum* was found only in the small intestine of *B. indica* from Thailand (Kalasin), although, *R. mindanensis mindanensis*, *R. rattus*, and *R. norvegicus* have been reported as the reservoir of the fluke in Southeast Asia (Cross and Basaca 1986, Namue and Wongsawad 1997, Salcedo and Glenn 2006).

P. muris. This small trematode is found in the small intestine of rats, dogs, and birds. Lymnaeid snails (*Stagnicola*) were reported as first intermediate hosts, whereas insect larvae and some fresh water fishes are potential second intermediate hosts (Hong et al. 1996, Waikagul and Thairungroj 1997). This fluke has been reported to be capable of infection in humans. In 1937, there was a report of experimental infection in humans by oral ingestion of metacercariae, the infective stage of *P. muris,* which was isolated from a freshwater snail. Consequently, eggs of the worm were detected in feces on day 9 after infection (McMullen 1937). Thereafter, some human cases were sporadically found in Japan and Korea (Asada et al. 1962, Hong et al. 1996). However, the symptomatology is not well defined, and human cases are yet to be reported from SEA. The present study showed that *M. caroli, M. cookii*, and *R. tanezumi* were infected by *P. muris*. In addition, this trematode was also found in *R. rattus* from the Philippines (Jueco and Zabala 1990) and *Rattus sladeni* from Vietnam (Nguyen 1991).

H. diminuta. This cestode is known as the "rat tapeworm" and is commonly found in the small intestine of rats and dogs (Asada 1923, Sirivichayakul et al. 2006). There have been several case reports of infection in humans worldwide (McMillan et al. 1971, Chitchang et al. 1978, Cohen 1989, Marangi et al. 2003, Rohela et al. 2012). Various species of arthropods, including fleas, beetles, caterpillars, and millipedes, were identified as the intermediate hosts (Heicher and Gallati 1978, Andreassen et al. 1999). Humans
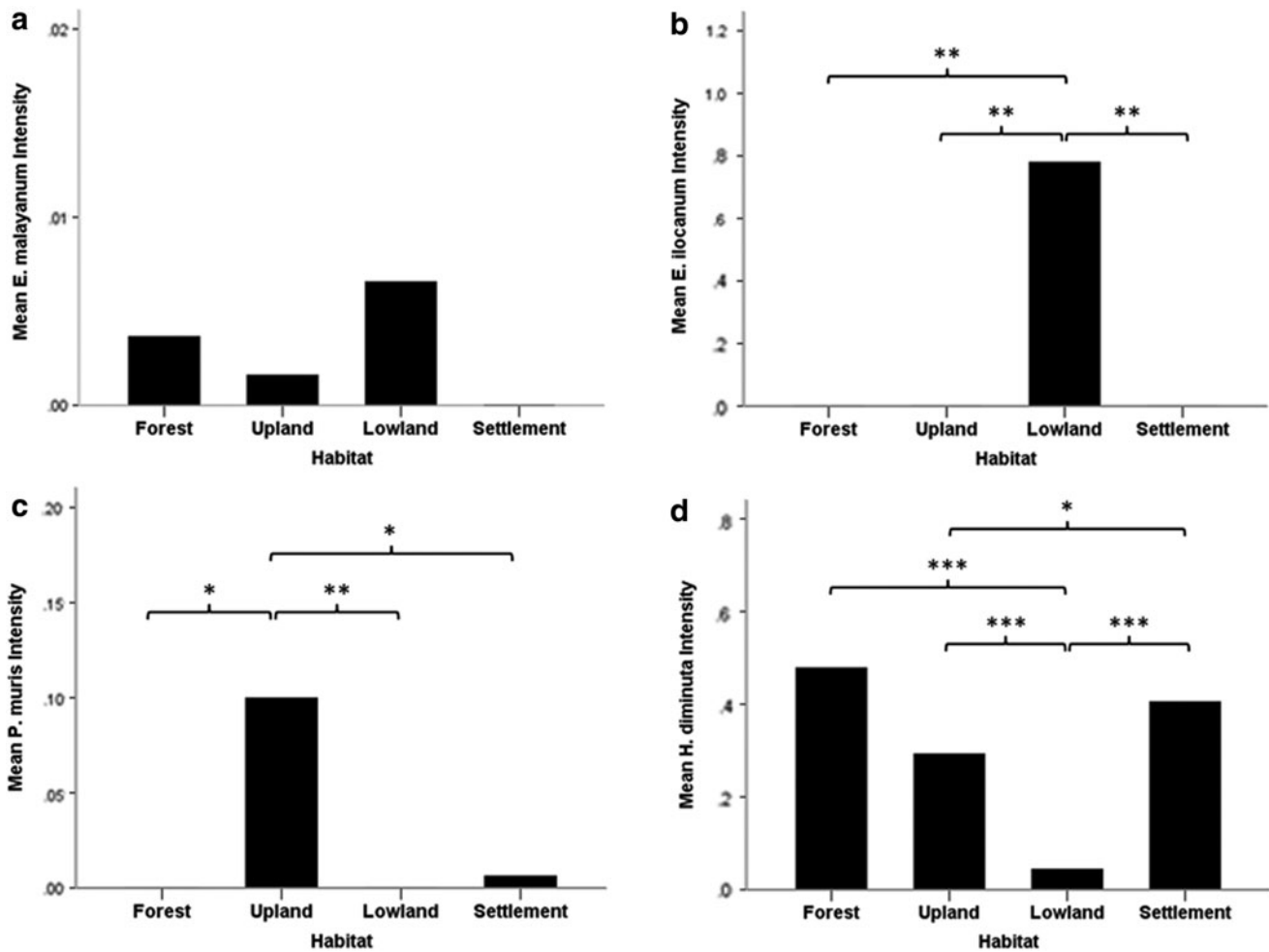
FIG. 3. Analysis of differences in zoonotic helminth intensity: (**a**) *Echinostoma malayanum*, (**b**) *Echinostoma ilocanum*, (**c**) *Plagiorchis muris*, (**d**) *Hymenolepis diminuta*, (**e**) *Hymenolepis nana*, (**f**) *Raillietina* spp., (**g**) *Cyclodontostomum purvisi*, and (**h**) *Moniliformis moniliformis*) among each habitat with multiple pairwise comparisons after Kruskal–Wallis test. (*) $p < 0.05$, (**) $p < 0.01$, (***) $p < 0.001$.

are infected by accidentally eating the cysticercoid-infected intermediate hosts found in food or, in the case of fleas, on the body. However, this parasite does not generally cause severe symptoms. Indeed, mild to moderate infection may cause no symptoms, whereas heavy infection can be accompanied by dizziness, anorexia, abdominal distress, and diarrhea (Markell et al. 1992, Waikagul and Thairungroj 1997). A number of murid rodent species have been reported as *H. diminuta* reservoirs in Southeast Asia: *Bandicota bengalensis*, *B. indica*, *B. savilei*, *Berylmys berdmorei*, *Berylmys bowersi*, *Leopoldamys edwardsi*, *Leopoldamys sabanus*, *Maxomys rajah*, *Maxomys surifer*, *M. caroli*, *M. cookii, Niviventer fulvescens*, and the rat species *Rattus annandalei*, *R. andamanensis*, *R. argentiventer, R. diardii, R. exulans, R. losea, R. molliculus*, *R. nitidus*, *R. norvegicus*, *R. rattus*, *R. tanezumi*, and *R. tiomanicus* (Betterton 1979, Leong et al. 1979, Sinniah 1979, Krishnasamy et al. 1980, Chenchittikul et al. 1983, Roberts 1991; Pham et al. 2001, Syed-Arnez and Mohd Zain 2006, Chaisiri et al. 2012, Pakdeenarong et al. 2014).

H. nana. The cestode *H. nana* is an intestinal parasite of rats, mice, and other rodents. It also known as the "dwarf

tapeworm," because it has the smallest adult stage of any cestode found in humans (Sedaf et al. 2013). The distribution of human cases is worldwide, but with a high prevalence in warm climates with poor sanitation rather than in colder climatic zones. It is particularly common in children (Voge and Heyneman 1957). Clinically, light infection with *H. nana* is asymptomatic, whereas heavy infection can produce mild symptoms such as weakness, anal pruritus, abdominal pain, and diarrhea (Sirivichayakul et al. 2000, Chero et al. 2007). This worm produces autoinfection and can directly complete its life cycle without the aid of any intermediate host. However, several species of fleas and beetles are known as facultative intermediate hosts in which the infective cysticercoid stage develops inside the arthropods awaiting ingestion by the definitive host. Humans become infected by direct contamination, by eggs, and less commonly by accidental ingestion of an infected beetle or flea. A high number of rodent species have been reported as reservoirs of this cestode: *Hapalomys delacouri*, *M. surifer*, *M. caroli*, *M. cervicolor*, *M. cookii*, *N. fulvescens*, *R. andamanensis*, *R. annandalei*, *R. exulans*, *R. norvegicus*, *R. diardii*, *R. losea*, *R. tanezumi*, and *R. tiomanicus* (Sinniah 1978, Krishnasamy et al. 1980,
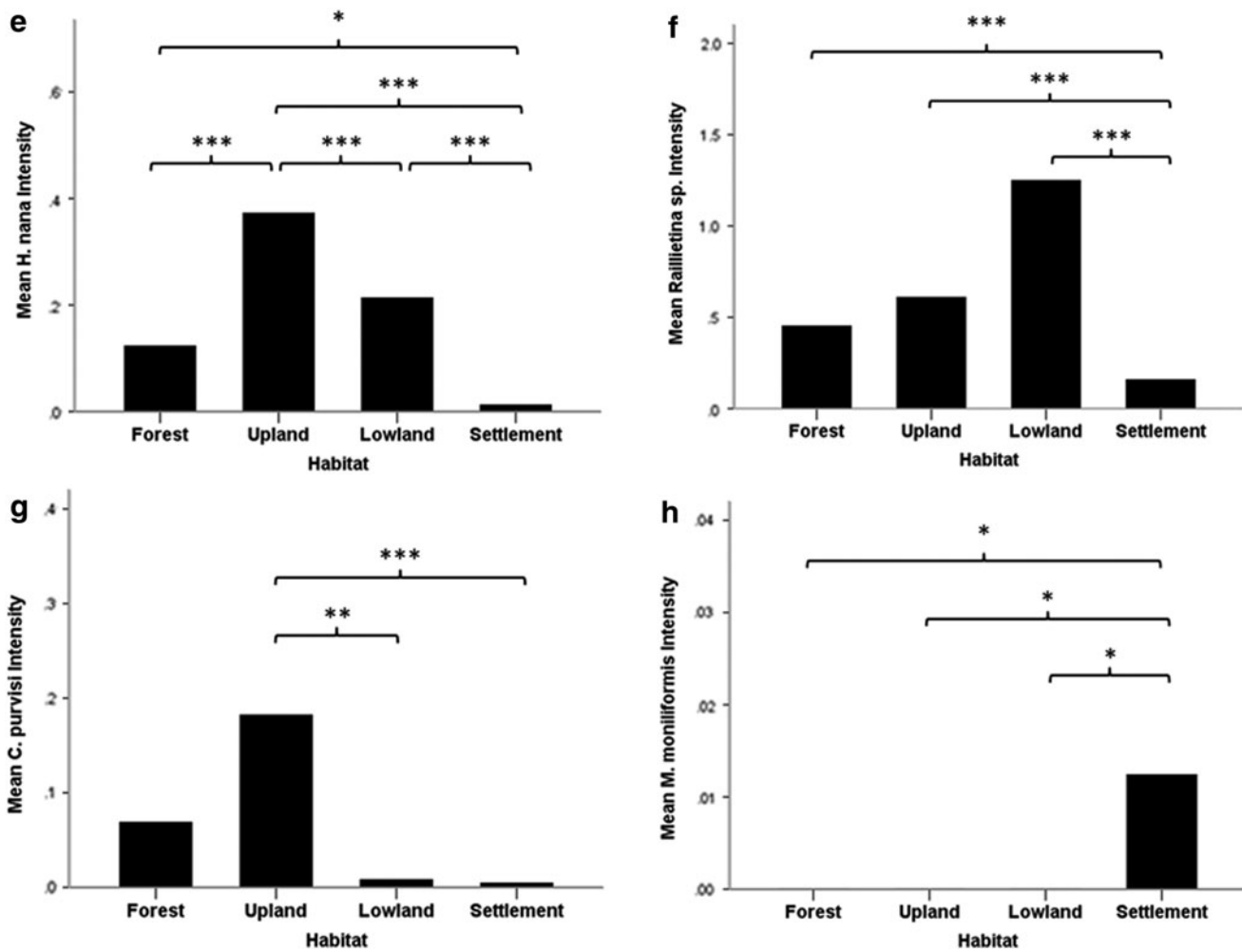
FIG. 3. (Continued).

Chenchittikul et al. 1983, Roberts 1991, Chaisiri et al. 2012, Pakdeenarong et al. 2014), demonstrating that *H. nana* is very successful at parasitizing a wide range of hosts.

Raillietina spp. This medium-sized tapeworm parasitizes mostly birds and sometimes humans. The parasite requires two intermediate insect hosts, such as beetles, ants, and cockroaches, to complete its life cycle. In Asia, there have been reports of human cases in Indian Ocean countries, China, Japan, and Thailand (Chandler and Pradatsundarasar 1957, Areekul and Radomyos 1970, Beaver et al. 1984). Humans are occasionally infected by ingesting cysticercoid-contaminated intermediate hosts. No symptoms have been recorded to date in humans infected by this cestode. Similar to *H. diminuta* and *H. nana*, several rodent species were reported as reservoirs of *Raillietina* spp. in Southeast Asia: *B. indica, B. savilei, B. berdmorei, B. bowersi, L. edwardsi, L. sabanus, M. surifer, M. caroli, M. cervicolor, M. cookii, Niviventer cremoriventer, N. fulvescens, R. losea, R. exulans, R. norvegicus, R. rattus,* and *R. tanezumi* (Areekul and Radomyos 1970, Betterton 1979, Namue and Wongsawad 1997, Chaisiri et al. 2012, Pakdeenarong et al. 2014).

C. purvisi. This nematode is known as the rat hookworm and is commonly found in the cecum of rats from Southeast Asia. This roundworm has a direct life cycle, similar to other hookworm species. The infective form is the third-stage larva that develops in the environment 4–5 days after hatching (Varughese 1973). Humans can be infected by consumption of improperly washed vegetables contaminated by the infective larvae (Sirivichayakul et al. 2006). However, there is only a single human case report (from a Thai man in Saraburi province, the central part of Thailand), and the parasite did not cause any symptoms in this patient (Bhaibulaya and Indra-ngarm 1975). Among rodents, several rat species can harbor *C. purvisi* infection: *B. indica, B. bowersi, L. sabanus, M.s surifer, M. rajah, Maxomys whiteheadi, N. cremoriventer, R. annandalei, R. argentiventer, R. bartelsii, R. hoffmanni, R. molliculus, R.mulleri, R. nitidus, R. sladeni, R. diardii,* and *R. tiomanicus* (Singh and Chee-Hock 1971, Varughese 1973, Wiroreno 1978, Sinniah 1979, Hasegawa and Syafruddin 1994, Chaisiri et al. 2012).

M. moniliformis. This acanthocephalan worm is found worldwide, usually infecting rodents, dogs, foxes, and cats as the definitive hosts. The parasite was clearly found in urban rodent species: *Rattus diardii, R. exulans, R. norvegicus, R. rattus,* and *R. tanezumi* (Leong et al. 1979, Chaisiri et al. 2012, Mohd Zain et al. 2012). Nevertheless, rodents from agricultural or periurban areas (*B. indica, R. annandalei, R.*
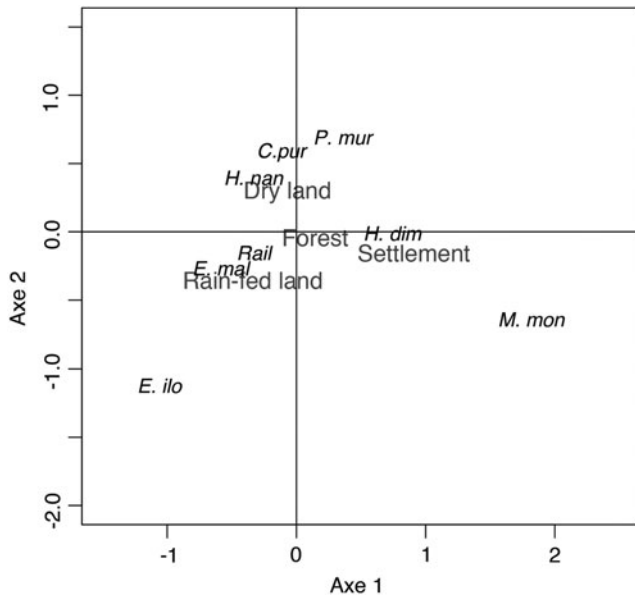
FIG. 4. Principal component analysis of helminth species association with the categorized habitats (*E. mal*, *Echinostoma malayanum*; *E. ilo*, *Echinostoma ilocanum*; *P. mur*, *Plagiorchis muris*; *H. dim*, *Hymenolepis diminuta*; *H. nan*, *Hymenolepis nana*; *Rail*, *Raillietina* spp.; *C. pur*, *Cyclodontostomum purvisi*; *M. mon*, *Moniliformis moniliformis*).

argentiventer, and *R. tiomanicus*) were also reported to be infected sporadically (Sinniah 1979). Similar to *Macracanthorhynchus hirudinaceus, M. moniliformis* is another acanthocephalan that has been reported in humans from the Middle East, Australia, Africa, and America (Moayedi et al. 1971, Al-Rawas et al. 1977, Counselman et al. 1989, Ikeh et al. 1992, Bettiol and Goldsmid 2000, Berenji et al. 2007, Salehabadi et al. 2008), whereas the incidence in Southeast Asia is still unknown. Beetles and cockroaches are recognized as intermediate hosts harboring the infective-stage larvae, the cystacanth. The definitive hosts, including humans, can become infected by consuming cystacanths. Although most infected

patients are asymptomatic, some reported symptoms include abdominal pain, dizziness, giddiness, and edema (Berenji et al. 2007, Salehabadi et al. 2008). Although humans infected with *M. moniliformis* have not been reported in Southeast Asia, there are several other reports of this acanthocephalan infection in rodents from the region, reflecting an important zoonotic risk.

The influence of habitat on the intensity of the zoonotic helminths

Due to the present findings, habitat acts as one of the factors that influence helminth infection in murid rodent hosts. In term of total zoonotic helminth intensity, rodents from human settlement habitat harbored significantly lower than the other habitat types (Fig. 2). This probably could be the effect of urbanization, which reduces biodiversity and parasite survival consequently; the more biodiversity is decreased, the more reduction there is in either the intermediate or definitive host for parasite. In addition, we also found that most of the zoonotic helminth species in the present study showed significant variation in intensity between different habitats (Fig. 3).

Rodents from dry land or nonflooded agricultural areas (*e.g.*, corn fields, cassava fields, orchards, grassland, or fallow) harbored a significantly higher intensity of *P. muris, H. nana*, and *C. purvisi* infections than the other habitats (Fig. 3c, e, g). In comparison with the other habitats, insects of agricultural importance might play a role as intermediate hosts for those parasites to complete their life cycle.

Lowlands or irrigated rice fields were the preferred habitat for the two echinostomatid flukes *E. malayanum* and *E. ilocanum*, showing significantly higher intensity than in the other habitats (Fig. 3a, b). This could be related to the biology of the gastropod intermediate hosts, which are commonly found in wetlands and rice fields (Lie et al. 1966, Ngoenklan et al. 2010).

Rodents from settlements, cities, or villages showed significantly lower intensity in various helminth species (*e.g.*, *H. nana, Raillietina* spp., and *C. purvisi*) than rodents from the other habitats (Fig. 3e, f, g). This may also be related to the low diversity of intermediate hosts in the urban/domestic
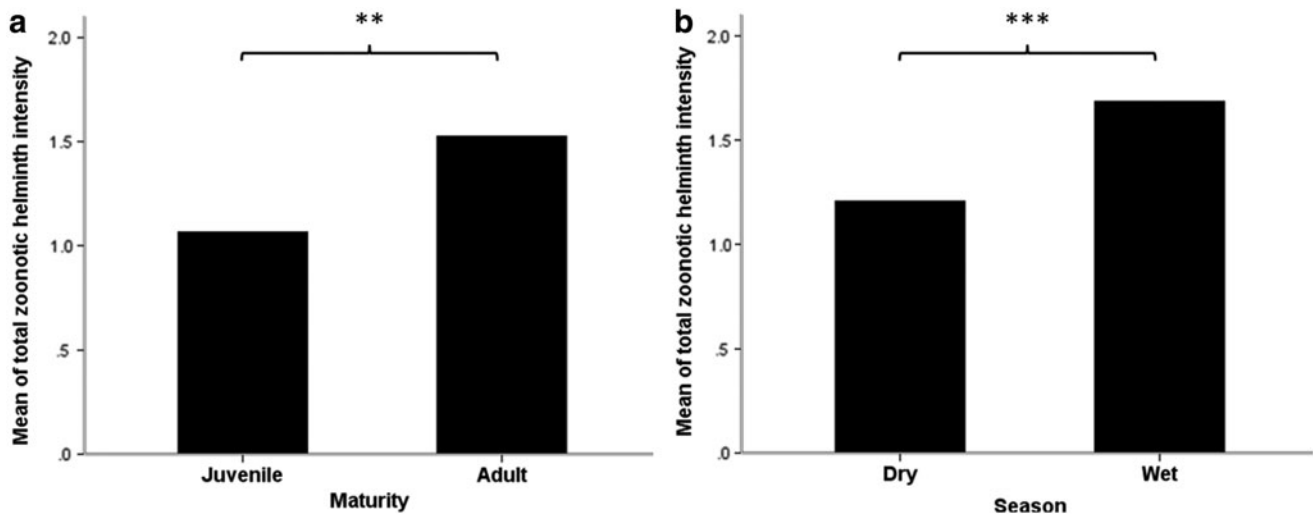

FIG. 5. Differences in total zoonotic helminth intensity with rodent maturity (**a**) and season (**b**) after comparison by a Mann–Whitney U-test. (*) $p < 0.05$, (**) $p < 0.01$, (***) $p < 0.001$.

area. Thus, people living in large villages or cities apparently face a lower risk of these helminth infections. Nevertheless, in the current study or our previous survey (Chaisiri et al. 2012), the acanthocephalan *M. moniliformis* was clearly found in urban or city rodents (Fig. 3h). These findings suggest that the life cycle of *M. moniliformis* is maintained by beetle or cockroach intermediate hosts living in domestic areas. Thus, rats in urban habitats appear to be an important reservoir of *M. moniliformis* infections for humans.

The influence of age, sex, and season on the intensity of zoonotic helminths

A number of researchers have reported the effect of host genders on the parasitic loads (Behnke et al. 2001, Kataranovski et al. 2011). Several publications have reported the trend of male bias in parasite infections, especially mammals (Poulin 1996, Zuk and McKean 1996, Klein 2004), whereas others have revealed the contradiction, with females having higher susceptibility (Behnke et al. 2008, Mohd Zain et al. 2012). There were some factors regarding sex bias in susceptibility to parasitic infection as linked to sex-differences in the production of sexual hormones that affect directly or indirectly to host's immunological response (Foldstad and Karter 1992, Poulin 1996); size difference, *i.e*, the larger sex (normally male) the more energy investment that reduces efficacy of immune function and tends to be more exposed or attractive for parasites (Moore and Wilson 2002); and sex-specific behavior inducing different exposure, such as a larger home range searching for food or mating that might lead to enhancing exposure to parasites (Tinsley 1989). It is definitely unclear to conclude in a global/broad-scale study that one gender is more susceptible for parasitic infection than another; a smaller-scale study should be better able to emphasize this research assumption. Because of the results from the present study, we found no difference in terms of total helminth intensity between male and female rodents. However, there were significant differences of individual helminth intensity between rodent genders. Female rodents harbored significantly higher intensities in *E. malayanum, E. ilocanum*, and *C. purvisi*, whereas no significantly higher helminth intensity was found in male rodents.

In terms of host maturity, total zoonotic helminth intensity was clearly higher in adult rodents than juveniles (Fig. 5a). This may be explained by the assumption that older hosts have a longer time to expose and accumulate the parasite infections throughout their life (Rossin et al. 2009, Kataranovski et al. 2011). Besides, adult rodents explore a larger area for foraging and breeding purposes and thus are potentially more in contact with infective stages of parasites.

Again, seasonal differences were observed for total zoonotic helminth intensity. Rodents captured during the wet season were infected with a higher number of zoonotic helminths than the rodents from the dry season (Fig. 5b). High humidity and moisture in the wet season promote a good rate of development and survival of parasite eggs and larvae in environment (O'Connor et al. 2007), inferring that infective stages of the parasites are likely to be more abundant and highly active than during the dryer period. Accordingly, we conclude that the wet season is potentially the risky period for humans to contract those zoonotic helminthiases.

The major rodent reservoir of the zoonotic helminths

Compared to the others rodent species in the present study, the Asian house rat *R. tanezumi* harbors the highest zoonotic helminth species richness (six out of eight). This rat is also the most captured by the project, reflecting a high density of this rodent species in this region. Unlike the others, *R. tanezumi* is the only species that is found ubiquitously in a large habitat range, from urban area to various wild or agricultural landscapes (Bordes et al. 2013). This rodent can act as a potential mechanical vector carrying the parasites across the different habitat types and spreading them into new environment. Due to the reasons given above, *R. tanezumi* is the main reservoir of rodent-borne zoonotic helminthiases in the Indochinese Peninsula.

Conclusions

A number of rodent-borne helminthiases were found in rodents from the Indochinese Peninsula. Most of these showed significant variation in intensity between different habitats. Rodents captured in the wet season harbored a significantly higher zoonotic helminth intensity than those trapped in the dry season, suggesting that the wet season represents a period of greater zoonotic risk. The Oriental house rat *R. tanezumi* is the most important reservoir of the zoonotic helminthiases and might carry and spread the parasites between habitats. Humans can be infected accidentally by ingestion of infective stage larvae contaminating vegetables and other foods or the environment. Finally, understanding the route of transmission, potentially riskier habitats, as well as good hygienic awareness will help in prevention of zoonotic helminthiases.

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