Parasitol Res (2009) 104:709–714
DOI 10.1007/s00436-008-1279-7

SHORT COMMUNICATION

Why do Siberian chipmunks *Tamias sibiricus* (Sciuridae) introduced in French forests acquired so few intestinal helminth species from native sympatric Murids?

Benoît Pisanu · Lise Lebailleux · Jean-Louis Chapuis

Received: 12 September 2008 / Accepted: 7 November 2008 / Published online: 3 December 2008

Abstract A lack of newly acquired species partly explains why introduced host species have poor specific parasite diversity. The intestinal helminth community from two native Murid host species, wood mice *Apodemus sylvaticus* [*Murinae*] (n=40), bank voles *Clethrionomys glareolus* [*Arvicolinae*] (n=42), and an introduced Sciurid, the Siberian chipmunk *Tamias sibiricus* (n=42), dominant in the rodent communities, was studied from three woody areas in the Ile-de-France region. Native gastrointestinal helminth fauna from mice and voles was formed by 12 taxa: ten nematodes, *Aonchotheca murissylvatici*, *Aonchotheca annulosa, Aspiculuris tetraptera, Eucoleus* sp., *Heligmosomoides glareoli*, *Heligmosomoides polygyrus*, *Mastophorus muris*, *Syphacia frederici*, *Syphacia stroma*, *Trichuris muris*, a Cestode and a Trematode. Two helminth taxa were imported by chipmunks from eastern Asia: *Brevistriata skrjabini* and *Strongyloides callosciureus*. Only *A. annulosa* was transferred to chipmunks from the native small rodent community. None of the 82 native murids harbored chipmunk helminths. The developmental ability of helminth according to host phylogenetic relatedness was the main driving force explaining the species composition of the helminth community between these sympatric native and introduced hosts.

B. Pisanu · L. Lebailleux · J.-L. Chapuis (✉)
Département Ecologie et gestion de la biodiversité,
Muséum National d'Histoire Naturelle,
UMR 5173 MNHN-CNRS-P6, 61 rue
Buffon, 75231 Paris cedex 05, France
e-mail: chapuis@mnhn.fr

Introduction

Introduced vertebrates have a lower parasite species diversity compared to their counterparts on their native area (Dobson and May 1986). Such a reduction in parasite diversity can result from the extinction of species very early after their host's introduction because (1) a small number of founding hosts brought a few number of parasite species with them; (2) of a lack of obligatory intermediate hosts or too constraining abiotic conditions; (3) of limitation in the acquisition of new parasite species (Torchin et al. 2003). While the first two hypotheses need both parasitic surveys from native populations soon after the introduction of hosts, the third can be empirically tested by comparing the parasitic cortege of co-inhabiting hosts that may transfer some of their parasites to introduced hosts.

The Siberian chipmunk *Tamias sibiricus* was introduced into suburban French forests less than 30 years ago and has now spread across several localities (Chapuis 2005). Chipmunks share a poor species diversity in intestinal helminth (Pisanu et al. 2007) and arthropods (hard ticks: Vourc'h et al. 2007; sucking lice: Beaucournu et al. 2008; fleas: Pisanu et al. 2008). For helminths, only two dominant species of nematodes and four other rare species have been found (Pisanu et al. 2007): one of the two dominant species, *Brevistriata skrjabini* (Schulz and Lubimov 1932) Durette-Desset 1976, is a nematode restricted to Northeastern Asiatic Sciurids, and the other, *Aonchotheca annulosa* (Dujardin 1845) Bain and Wertheim 1981 is a nematode that develops in a wide spectrum of compatible host species, parasitizing numbers of Western European boreal mammals (Moravec 2000; Pisanu et al. 2007).

This study is based on the helminth survey of the two dominant native species of terrestrial rodents co-inhabiting with introduced chipmunks on three woody localities of the

Ile-de-France region. This paper aims to understand why Siberian chipmunks acquired so few intestinal helminth species when introduced into French forests.

Materials and methods

Ninety-four rodents were analyzed, trapped from three locations in late May/early July. This sample includes: ten wood mice *Apodemus sylvaticus* and 12 bank voles *Clethrionomys glareolus* from the Forest of Sénart (48°39′ N, 02°29′ E; 3,200 ha) in 2004 and 2005. Thirty rodents (15 of both species) were analyzed from the urban Park of Henri Sellier (48°46′ N, 02°16′ E; 26 ha) in 2006 and 15 of both species from the Wood of Verneuil-sur-Seine (48°59′ N, 01°56′ E; 400 ha) in 2007. Additionally, 12 chipmunks were analyzed which had been trapped in the same months in 2007 on the Wood of Verneuil-sur-Seine, completing a previous helminth survey in this locality (n=3, see Pisanu et al. 2007). Rodents were live-trapped and killed by cervical dislocation, then frozen at −20°C before analysis. The Forest of Sénart rodents were autopsied in the field and the entire digestive tract was removed and fixed in ethanol 70°C. Identification of Murid rodents was based on Le Louarn and Quéré (2003). Helminths were searched for by dissection of the complete gut walls and lumen, from esophagus to rectum, and counted using binocular lenses (×10–60). Species identification was done by morphological analysis using a microscope equipped with a *camera lucida*, and was based on, for the genus *Aonchotheca* Lopez-Neyra 1947, *sensu* Moravec (1982) and *Eucoleus* Dujardin 1845 *sensu* Moravec (1982) to the descriptions by Roman (1951), Bain and Wertheim (1981), Justine and de Roguin (1990), Pisanu and Bain (1999), and Moravec (2000); for the genus *Trichuris* Roederer 1781 by Feliu et al. (2000) ; Genus *Brevistriata* Durette-Desset 1971 by Durette-Desset (1970, 1976) ; Genus *Heligmosomoides* Hall 1916 by Durette-Desset (1971) and Biserkov et al. (1998); Genus *Syphacia* Seurat 1916 *sensu* Hugot 1988 and *Aspiculuris* Schulz 1924 by Roman (1951) and Quentin (1971a); Genus *Mastophorus* Gmelin 1790 by Quentin (1969; 1971b); Genus *Strongyloides* Grassi 1879 by Sato et al. (2007).

Prevalence and mean number of worms per infected host, i.e., mean intensity of infection, along with their 95% confidence intervals, were calculated using a bootstrapped method provided by the Quantitative Parasitology 3.0 software (Reiczigel and Rózsa 2005). Prevalence was compared between sites using the Fisher's exact test and mean intensity was compared using the Mood's median test.

Results

A. annulosa was found in the small intestine of all the hosts species analyzed (Table 1). In the Forest of Sénart sample, it was found in one wood mouse (ten worms) and in eight chipmunks with a mean intensity of two worms (range in counts one to seven worms), but not in voles. There was neither difference in prevalence (P_{Fisher}=0.21) between species, nor intensities (P_{Mood}=0.44). All host species harbored *A. annulosa* in the Park Henri Sellier sample: 13 mice with a mean intensity of 15 worms (range 1–51), seven voles with a mean intensity of 11 worms (2–21), and four chipmunks with a mean of 117 worms (3–431), and no differences in prevalence (P_{Fisher}=0.07) and mean intensity (P_{Mood}=0.73) between hosts. In the Wood of Verneuil-sur-Seine sample, all hosts also harbored *A. annulosa*: five chipmunks with a mean intensity of four worms (between 1 and 7), two mice (2; 39), and two voles (6; 11), without differences in prevalence (P_{Fisher}=0.45) or mean intensity (P_{Mood}=1.00). *A. annulosa* was significantly more frequent in wood mice on the Park Henri Sellier than on the other sites analyzed (P_{Fisher}<0.01) but not in mean intensity (P_{Mood}=1.00). There were no differences in chipmunks between sites (P_{Fisher}=0.26; P_{Mood}= 0.08), as in bank voles (P_{Fisher}=0.11; P_{Mood}=1.00).

Mastophorus muris was found in the stomach of wood mice and bank voles. Only one vole had one worm in the Sénart sample (Table 1). In the Henri Sellier sample, four mice had *M. muris* with a mean intensity of two worms (one to two) and six voles with a mean of six worms (1–16), without differences between species (P_{Fisher}=0.70; P_{Mood}=0.20). In the Verneuil-sur-Seine sample, six mice had *M. muris* with a mean intensity of three worms (one to five), and 14 voles with a mean of seven worms (1–34). Voles were more frequently infected than mice (P_{Fisher}< 0.01), but there were no differences in mean intensity of infection by *M. muris* (P_{Mood}=1.00). There were no differences in mice between sites (P_{Fisher}=0.70; P_{Mood}= 0.20); voles were more frequently infected in Verneuil-sur-Seine than in Sellier (P_{Fisher}<0.01), and no differences were found in mean intensity between sites (P_{Mood}=1.00). *M. muris* was not found in chipmunks.

Aonchotheca murissylvatici was found in the small intestine of two mice from Sénart (one and two worms). This worm was found encysted in the stomach of eight voles in Sénart with a mean of 35 worms (5–100), and 11 in Henri Sellier with a mean of 159 worms (40–500), but not in Verneuil-sur-Seine. There were no differences in infection in voles between sites (P_{Fisher}=1.00; P_{Mood}=0.06). *A. murissylvatici* was not found in chipmunks.

All the other helminth species were found in a single host species. *Heligmosomoides polygyrus* was found only in the small intestine of wood mice: five in Sénart with a

Table 1 Mean intensity (mI) of infection, followed by the 95% confidence interval in parentheses, and number of hosts infected (*n*) by helminth in rodents on the Forest of Sénart, the Park of Henri Sellier, and the Wood of Verneuil-sur-Seine

Localities	LC	Sénart		Henri Sellier		Verneuil-sur-Seine	
Helminth species per host species		*n*	mI (95CI)—[counts]	*n*	mI (95CI)—[counts]	*n*	mI (95CI)—[counts]
Wood mice, *A. sylvaticus*		*N=10*		*N=15*		*N=15*	
Heligmosomoides polygyrus	M	5	[1; 2; 13; 19; 32]	14	7 (5–13)	15	32 (19-52)
Syphacia stroma	M	2	[1; 123]	14	24 (15–39)	14	85 (48-149)
Aonchotheca annulosa	U	1	[10]	13	15 (9–25)	2	[2; 39]
Cestoda sp.	H	2	[1; 1]	10	4 (3–6)	1	[1]
Trichuris muris	M	3	[1; 1; 2]	8	2 (1–3)	0	-
Mastophorus muris	H	0	–	4	[1; 1; 2; 2]	6	3 (2-4)
Syphacia frederici	M	4	[1; 20; 74; 108]	1	[3]	0	-
Eucoleus sp. (? *bacillatus*)	U	2	[1; 1]	3	[2; 3; 5]	0	-
Aspiculuris tetraptera	M	3	[1; 1; 4]	0	–	0	-
Aonchotheca murissylvatici	U	1	[1]	1	[2]	0	-
Trematoda sp.	H	2	[1; 6]	0	–	0	-
Bank voles, *C. glareolus*		*N=12*		*N=15*		*N=15*	
Mastophorus muris	H	1	[1]	6	6 (2–11)	14	7 (4–14)
Heligmosomoides glareoli	M	10	3 (2–5)	8	5 (3–7)	1	[2]
Aonchotheca murissylvatici	U	8	35 (20–60)	11	159 (95–265)	0	–
Aonchotheca annulosa	U	0	–	7	11 (5–16)	2	[6 ; 11]
Cestoda sp.	H	0	–	1	[1]	5	[1; 1; 1; 3; 3]
Trichuris sp.	M	1	[1]	0	–	0	–
Siberian chipmunks, *T. sibiricus*		*N=22*[a]		*N=5*		*N=15*	
Brevistriata skrjabini	M	20	44 (27–79)	3	[20; 30; 38]	15	175 (51–632)
Aonchotheca annulosa	U	8	2 (1–4)	4	[3; 15; 16; 431]	5	[1; 1; 2; 7; 7]
Strongyloides callosciureus	M	0	–	0	–	8	7 (5–9)
Trichuris sp.	M	4	[1; 1; 1; 1]	0	–	0	–
Trichostrongyloidea sp.	M	0	–	0	–	3	[1; 2; 4]
Oxyuroidea sp.	M	1	[1]	0	–	0	–
Ascaroidea sp.	U	0	–	0	–	1	[1]

LC Life-cycle of helminths, *M* Monoxenous, *H* Heteroxenous, *U* Unknown. Worm counts are indicated between brackets.
[a] Re calculated from Pisanu et al. (2007).

mean of 13 worms (1–32), 14 in Sellier with a mean of 7 worms (1–28), and all mice trapped in Verneuil-sur-Seine with a mean of 32 worms (1–119). Mice in Sénart were significantly less frequently infected by *H. polygyrus* than in the two other locations ($P_{\text{Fisher}}<0.01$), without any significant difference in mean intensity of infection between sites ($P_{\text{Mood}}=0.13$). *Syphacia* (*Syphacia*) *stroma* was found in two mice in Sénart (1 and 123 worms), in 14 mice in Henri Sellier with a mean of 24 worms (1–73), and 14 in Verneuil-sur-Seine with a mean of 85 worms (1–119). Mice in Sénart were significantly less frequently infected by *S. stroma* than in the two other localities ($P_{\text{Fisher}}<0.01$), without any significant difference in mean intensity of infection between sites ($P_{\text{Mood}}=0.35$). *Trichuris muris* was found in three mice in Sénart (one, one and two worms) and eight mice in Henri Sellier with a mean of two worms (one to four), but not in Verneuil-sur-Seine. No difference between sites was found in *T. muris* infection in mice ($P_{\text{Fisher}}=0.41$; $P_{\text{Mood}}=1.00$). *Syphacia* (*Syphacia*) *frederici* was found in a single mouse in Henri Sellier (three worms), and in four mice in Sénart (1, 20, 74 and 108 worms). *Eucoleus* sp. (? *bacillatus*) was found in three mice in Sellier (two, three, and five worms) and in two mice in Sénart, each harboring a single worm encysted in the stomach wall. *Aspiculuris tetraptera* was found in only three mice (one, one, and four worms) in Sénart.

Heligmosomoides glareoli was found in the small intestine of one bank vole (two worms) in Verneuil-sur-Seine, in eight voles on Sellier with a mean of five worms (two to ten), and in ten voles in Sénart with a mean of four worms (1–11). Voles in Verneuil-sur-Seine were significantly less frequently infected by *H. glareoli* than in the two other locations ($P_{\text{Fisher}}<0.01$), without any significant difference in mean intensity of infection between sites ($P_{\text{Mood}}=0.50$). Only one specimen belonging to the genus *Trichuris* was found in the cecum of a vole in Sénart.

B. skrjabini (Schulz and Lubimov 1932) Durette-Desset 1976 was found in the small intestine of three chipmunks in

Sellier (20, 30, and 38 worms), 15 in Verneuil-sur-Seine with a mean of 175 worms (1–1,819), and 20 in Sénart with a mean of 44 worms (1–225). There was no difference in prevalence in *B. skrjabini* in chipmunks according to site (P_{Fisher}=0.08), and chipmunks in Verneuil-sur-Seine were more intensely infected by *B. skrjabini* than in the other sites (P_{Mood}=0.05*). Strongyloides callosciureus* (Sato et al. 2007) was found only in eight chipmunks in Verneuil-sur-Seine, with a mean of seven worms (four to ten). In the Sénart sample, four chipmunks hosted a Trichuroid female in their cecum, and one had an Oxyurid male also in the cecum. One chipmunk had an Ascaroid male in the duodenum at Verneuil-sur-Seine, and three chipmunks had immature stages of a Trichostrongyloid (one, two and four worms) in the small intestine.

Unidentified cestodes Cyclophyllidea were found in the small intestine of a mouse in Verneuil-sur-Seine (one worm), in Sénart (two mice each infected by a single worm), and in Henri Sellier, where ten mice harbored a mean of four worms (three to six). One vole had one specimen of a Cestode. An unidentified Trematode was found in the small intestine of two mice (one and six worms) from Sénart.

Discussion

Introduced chipmunks acquired only one of the species shared by sympatric native Murid species that dominate in the rodent community: *A. annulosa*. This nematode was the third most often identified in the rodent's helminth community, with a total of 849 worms counted. It infects a very wide number of host species in Western Europe (Pisanu et al. 2007), mainly rodents and even insectivores or primates (Moravec 2000). This result highlights that such a generalist helminth species (i.e., with a wide spectrum of compatible host species; Combes 1995) is more prone to invade new host species, providing its taxonomic position is valuable (for the genus *Aonchotheca*, see Moravec 1982; Pisanu and Bain 1999). Its life-cycle is unknown.

Eleven other helminth species were restricted to the native Murid species. Among these, at least three are heteroxenous species: *M. muris*, and the Platyhelminths. Six are monoxenous species, *H. polygyrus*, *S. stroma*, *T. muris*, *S. frederici*, and *A. tetraptera*. The life cycles of the Capillariids nematodes *Eucoleus* sp. (? *bacillatus*) and *A. murissylvatici* are unknown.

M. muris is commonly transferred between wood mice and bank voles. This nematode is acquired from the consumption of insect prey which is an obligate intermediate host (Anderson 1992). *M. muris* was not found in chipmunks, although these terrestrial Sciurid are omnivorous (Kawamichi 1980), and prey on several insect and snail species in the Forest of Sénart (J.-L. Chapuis, unpublished). This result confirms that heteroxenous helminth can accidentally develop at least in related host species at the family level, i.e. Murid rodents for *M. muris*.

Unidentified trematodes were only found in wood mice in Sénart. This result highlights the importance of local peculiarities in helminth community composition of rodents, such as in wood mice (Abu-Madi et al. 2000; Eira et al. 2006) or bank voles (Behnke et al. 2001). These platyhelminth species were not found in chipmunks, indicating that heteroxeny is not a key condition of helminth biology for successful host transfer.

All other helminth species are monoxenous nematodes, which can be seen as specific of their host at the subfamily or genus level: *H. polygyrus*, *S. stroma*, *T. muris*, *S. frederici*, and *A. tetraptera* in Murinae (i.e. *Apodemus* spp., *Mus* spp.; Anderson 1992), and *H. glareoli* in Arvicolinae (*Clethrionomys* spp., *Microtus* spp.; Biserkov et al. 1998). The life cycle of *Eucoleus* sp. (? *bacillatus*) and *A. murissylvatici* is unknown. However, *Eucoleus* spp. has been reported as being specific to the genus level within the *Murinae* (Roman 1951; Bain and Wertheim 1981; Moravec 2000). *A. murissylvatici* only very occasionally infects hosts in *Murinae*, as in Sénart. It is more frequently and intensely found in *C. glareolus* (Moravec 2000). According to the observation in this study, bank voles can be considered as primary host for *A. murissylvatici*. Thus, reduced spectrum of compatible host species available to fully develop must explains why these helminths were not found in chipmunks.

Chipmunks imported two nematode species in Ile-de-France: *B. skrjabini* and *S. callosciureus*. *B. skrjabini* is most probably a direct life cycle nematode, and it is restricted to Sciurid hosts in Eastern Asia (Pisanu et al. 2007). *S. callosciureus* was missed in the previous study. This nematode was recently described from feral Pallas's squirrels *Callosciurus erythraeus* introduced as zoo or park animals from Taiwan, and captive Plantain squirrels *Callosciurus notatus* originating from Malaysia and sold in Japan in 2004–2005 (Sato et al. 2007). Again, affinities of this nematode species with the Sciurids could explain why they were not found in the Murid rodents co-inhabiting with chipmunks in Ile-de-France.

A total of 13 nematode specimens belonging to at least five taxa were also found in nine chipmunks that could not be fully identified at the species level. These represent accidental infections that may have been acquired from other hosts species inhabiting the localities investigated here. In the case of seven immature stages of Trichostrongyloidea, a male was observed which did not corresponded to the species found in native rodents. The four females *Trichuris* sp. found in the cecum of four chipmunks in Sénart may be accidental infection by *T. muris*, which is

mainly found in *A. sylvaticus* on this locality. Only molecular identification could help in identifying these specimens, as morphology alone remains insufficient to discriminate between *Trichuris* sp. from Murid rodents (Feliu et al. 2000).

At least 14 helminth species were found in the native small rodents living sympatrically in the three woody localities investigated in Ile-de-France, of which only one was transferred to introduced chipmunks: *A. annulosa*, a generalist nematode species. The lack of inter-transmission by the other species found in these rodents is mainly explained by the ability for helminth to develop only in phylogenetically related host species (Klimpel et al. 2007). These results are in accordance with other studies on the parasite diversity of these introduced Sciurid (Pisanu et al. 2008; Beaucournu et al. 2008) and more largely with introduced rodents (Asakawa 2005). If native host species are threatened by parasites imported with introduced hosts (Prenter et al. 2004; Smith and Carpenter 2006), then careful attention should be paid to closely related native host species, like European red squirrels *Sciurus vulgaris* L., that live sympatrically with introduced chipmunks in French forests (Pisanu et al. 2007, 2008).

Acknowledgements We wish to thank F. Bart, C. Huchery, C. Jérusalem, M. Laprun, G. Le Flohic, J. Prieur, and M. Roussel for their help in the parasitological analysis. C. Huchery and G. Ainsworth (Charles Darwin University, Australia) kindly improved the English version of the ms. This work was funded by the Région Ile-de-France, the Conseil Général des Hauts-de-Seine, and the Office National des Forêts.

References

Abu-Madi MA, Behnke JM, Lewis JW, Gilbert FS (2000) Seasonal and site specific variation in the component community structure of intestinal helminths in *Apodemus sylvaticus* from three contrasting habitats in south-east England. J Helminthol 74:7–15

Anderson RC (1992) Nematode parasites of vertebrates: their development and transmission. C.A.B. International, U.K

Asakawa M (2005) Perspectives of host-parasite relationships between rodents and nematodes in Japan. Mamm Study 30: S95–S99

Bain O, Wertheim G (1981) Helminthes d'Oiseaux et de Mammifères d'Israël. IX. Compléments morphologiques sur quelques *Capillaria* (Nematoda, Trichinelloidea). Bull Mus natn Hist nat 3:1061–1075

Beaucournu J-C, Pisanu B, Chapuis J-L (2008) *Enderleinellus tamiasis* Fahrenholz, 1916 (Anoplura- Enderleinellidae), espèce importée, implantée et nouvelle pour la faune de France. Parasite 15:175–178

Behnke J, Barnard CJ, Bajer A, Bray D, Dinmore J, Frake K, Osmond J, Race T, Sinski E (2001) Variation in the helminth community structure in bank voles (*Clethrionomys glareolus*) from three comparable localities in the Mazury Lake District region of Poland. Parasitol 123:401–414

Biserkov VY, Genov T, Hadjinikolova RI (1998) *Heligmosomoides glareoli* Baylis, 1928 (Nematoda: Heligmosomidae): redescription and synonymy. Syst Parasitol 41:179–186

Chapuis J-L (2005) Répartition en France d'un animal de compagnie naturalisé, le Tamia de Sibérie (*Tamias sibiricus*). Rev Ecol (Terre Vie) 60:239–253

Combes C (1995) Interactions durables : Ecologie et évolution du parasitisme. Masson Ed, Paris

Dobson AP, May RM (1986) Patterns of invasion by pathogens and parasites. In: Mooney HA, Drake JA (eds) Ecology of biological invasions of North America and Hawaii. Springer, Berlin, Heidelberg, New York, pp 58–76

Durette-Desset M-C (1970) *Brevistriata bergerardi*, nouveau Nématode Héligmosome, parasite d'un écureuil de Corée. Bull Mus natn Hist nat 42:419–423

Durette-Desset M-C (1976) *Brevistriatinae* (Nematoda: Heligmosomidae) I. Compléments morphologiques à l'étude d'espèces connues. Bull Mus natn Hist nat 270:685–692

Eira C, Torres J, Vingada J, Miquel J (2006) Ecological aspects influencing the helminth community of the wood mouse *Apodemus sylvaticus* in Dunas de Mira, Portugal. Acta Parasitol 51:300–308

Feliu C, Spakulová M, Casanova JC, Renaud F, Morand S, Hugot J-P, Santalla F, Durand P (2000) Genetic and morphological heterogeneity in small rodent whipworms in Southwestern Europe: characterization of *Trichuris muris* and description of *Trichuris arvicolae* n. sp. (Nematoda: Trichuridae). J Parasitol 86:442–449

Hugot J-P (1988) Les Nématodes *Syphaciinae*, parasites de Rongeurs et de Lagomorphes. Taxonomie, zoogéographie, évolution. Mém Mus natn Hist nat (A) 141:1–153

Justine J-L, de Roguin L (1990) *Capillaria muryssylvatici* (Nematoda, Capillariinae), parasite d'un Rongeur du Baluchistan iranien. Bull Mus natn Hist nat (A) 12:19–33

Kawamichi M (1980) Food, food hoarding and seasonal changes of Siberian chipmunks. Japanese J Ecol 30:211–220

Klimpel S, Förster M, Schmahl G (2007) Parasites of two abundant sympatric rodent species in relation to host phylogeny and ecology. Parasitol Res 100:867–875

Le Louarn H, Quéré J-P (2003) Les Rongeurs de France. Faunistique et biologie. I.N.R.A. Ed, Paris

Moravec F (1982) Proposal of a new systematic arrangement of the nematodes of the family Capillariidae. Folia Parasit 29:119–132

Moravec F (2000) A review of capillariid and trichosomoidid nematodes from mammals in the Czech Republic and the Slovak Republic. Acta Soc Zool Bohem 64:271–304

Pisanu B, Bain O (1999) *Aonchotheca musimon* n. sp. (Nematoda: Capillariinae) from the mouflon *Ovis musimon* in the sub-Antarctic Kerguelen archipelago, with comments on the relationships with *A. bilobata* (Bhalerao, 1933) Moravec, 1982 and other species of the genus. Syst Parasitol 43:17–27

Pisanu B, Jérusalem C, Huchery C, Marmet J, Chapuis J-L (2007) Helminth fauna of the Siberian chipmunk, *Tamias sibiricus* Laxmann (Rodentia, Sciuridae) introduced in suburban French forests. Parasitol Res 100:1375–1379

Pisanu B, Marmet J, Beaucournu J-C, Chapuis J-L (2008) Diversité du cortège en Siphonaptères chez le tamia de Sibérie (*Tamias sibiricus* Laxmann) introduit en forêt de Sénart (Ile-de-France). Parasite 15:35–43

Prenter J, MacNeil C, Dick JTA, Dunn AM (2004) Roles of parasites in animal invasions. Trends Ecol Evol 19:385–390

Quentin J-C (1969) Cycle biologique de *Protospirura muricola* Geodelst, 1916 (Nematoda: Spiruridae). Ann Parasitol Hum Comp 44:485–504

Quentin J-C (1971a) Sur les modalités d'évolution chez quelques lignées d'Helminthes de Rongeurs Muroidea. Cah. O.R.S.T.O.M 9:103–176

Quentin J-C (1971b) Morphologie comparée des structures céphaliques et génitales des Oxyures du genre *Syphacia*. Ann Parasitol Hum Comp 46:15–60

Reiczigel J, Rózsa L (2005) Quantitative parasitology 3.0. Budapest. (http://bio.univet.hu/qp/qp.htm)

Roman E (1951) Etude écologique et morphologique sur les acanthocéphales et les nématodes parasites des rats de la région lyonnaise. Mém Mus natn Hist nat (A) 2:49–270

Sato H, Torii H, Une Y, Ooi H-K (2007) A new Rhabditoid nematode species in Asian Sciurids, distinct from *Strongyloides robustus* in north American Sciurids. J Parasitol 93:1476–1486

Smith KF, Carpenter SM (2006) Potential spread of introduced black rat (*Rattus rattus*) parasites to endemic deer mice (*Peromyscus maniculatus*) on the California Channel Islands. Diversity Distrib 12:742–748

Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. Nature 421:628–630

Vourc'h G, Marmet J, Chassagne M, Bord S, Chapuis J-L (2007) *Borrelia burgdorferi* sensu lato in Siberian Chipmunks (*Tamias sibiricus*) introduced in suburban forests. Vector-Borne Zoonotic Dis 7:637–642