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Short communication

Macroparasites of Pallas's squirrels (*Callosciurus erythraeus*) introduced into Europe

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ABSTRACT

Introduced pets released *in natura* can lead to sanitary risks for native fauna and humans. We analysed the macroparasite fauna of a total of 49 Pallas's squirrels, *Callosciurus erythraeus*, from two populations introduced into urbanised areas in Europe ($n = 16$ ♀ and 13 ♂ from Antibes, France, 43°33′N–7°7′E; $n = 11$ ♀ and 9 ♂ in from Dadizele, Belgium, 50°52′N–3°5′E). Of the 185 identified ectoparasites from Antibes, 183 were sucking lice *Enderleinellus kumadai*, with male squirrels 10 times more intensely infested than females. The flea *Nosopsyllus fasciatus* was found on two hosts. No hard ticks were recovered. Of the 131 arthropods specimens from Dadizele, 45 belonged to *E. kumadai*, with male squirrels three times more intensely infested than females. Eighty-six arthropods belonged to another sucking louse, *Hoplopleura erismata*, with males infested twice as intensely as females. No fleas or hard ticks were found. We only found 12 immature *Hymenolepis* sp. cestodes in the small intestine of three squirrels from Antibes and two immature *Mastophorus* sp. female nematodes in the stomach of a squirrel from Dadizele. We found no other helminths in the body cavity, heart, lung, liver, kidney or bladder. The macroparasite fauna of these two squirrel populations is consistent with what is expected from an introduced host, i.e., a few species dominated by specialist taxa imported with founders. The scarcity of other rodent species in the urbanised areas where Pallas's squirrels were sampled may explain the low variety of newly acquired macroparasites. The discrepancy in sucking lice infestations between males and females could be due to differences in either behaviour or physiology in this non-sexually dimorphic host. Based on the macroparasites found in this study, we expect minimal sanitary risks for both native fauna and humans in urbanised habitats such as those in our study.

1. Introduction

Imported pets carry parasites from their native area (Ide et al., 2000; Yokoyama et al., 2003; Pisanu et al., 2007; Beaucournu et al., 2008; Hasegawa et al., 2008). If released, introduced hosts can transfer parasites to native host species (Asakawa, 2005; Smith and Carpenter, 2006; Bordes et al., 2007). There is also an increase in sanitary risks to humans because these pets may be more susceptible to becoming infected by pathogens through the acquisition of local vector-borne arthropods (Irwin, 2002; Beugnet and Marié, 2009). This risk has been identified for introduced squirrels (Craine et al., 1995; Shinozaki et al., 2004; Vourc'h et al., 2007; Pisanu et al., 2010). Additionally, these alien hosts can acquire new parasites originating from native hosts (Torchin and Mitchell, 2004;

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Asakawa, 2005; Pisanu et al., 2008, 2009). These newly acquired parasite species are often characterized by the ability of developing in a wide array of hosts, or when introduced hosts are phylogenetically close to native cohabiting host species (Asakawa, 2005; Tompkins and Poulin, 2006; Pisanu et al., 2009).

The Pallas's squirrel, *Callosciurus erythraeus*, is native to South-eastern Asia (Duckworth et al., 2008). It was introduced in the late 1960s (J.-M. Gourreau, personal communication) or before 1974 according to Jouanin (1986, 1992; see also Gerriet, 2009) to Cap d'Antibes (Alpes-Maritimes, France). It was introduced in the early 2000s to Dadizele (Belgium; Stuyck, 2009). These populations are two of the three known ones that have been established in Western Europe; there is also a small population in the Netherlands (Dijkstra et al., 2009). The origin of these populations and the number of founders are unknown. However, the Belgian and French populations probably originated from a single introduction event.

We studied the macroparasite species of the French and Belgian populations of Pallas's squirrel to evaluate the sanitary hazards to native fauna and humans from imported or newly acquired taxa (Shinozaki et al., 2004; Vourc'h et al., 2007; Pisanu et al., 2010). We expect the parasitic population, including Arthropods and Helminths, to be made up by two groups of parasites: (1) specialist taxa imported with founder hosts, and (2) local generalist parasites.

2. Materials and methods

We studied 49 Pallas's squirrels: 20 individuals collected in an urban park in Dadizele (Flanders, Belgium, 50°51′N–3°5′E) during an eradication attempt in February until April 2008 (Stuyck, 2009); 29 squirrels from Alpes-Maritimes (France); 27 from the park of the Villa Thuret (Antibes, 43°34′N–7°7′E) between February and June 2009; and two from the Bois des Encourdoules (Vallauris, 6 km Northwest, 43°35′N, 7°3′E), one in March and one in June 2009. Belgian specimens were live-trapped, euthanised and entire carcasses were kept frozen at −20 °C. French specimens were live-trapped, euthanised and eviscerated in the field. The gut, from oesophagus to rectum, was stored in 70% ethanol and carcasses were then immediately frozen at −20 °C in individual plastic bags for later examination of ectoparasites. Bodies were weighed (with viscera) to the nearest gram, and we measured head-body, tail and hind foot lengths (Berry, 1970) to the nearest millimetre.

We examined the entire body for the presence of ectoparasites using a stereo-microscope. We also examined the abdominal cavity, heart, lungs, liver, kidneys and bladder for internal helminths. Lumen and walls from oesophagus to rectum were examined for intestinal helminths. Specimen identifications refer to the following: the cestode family Hymenolepididae Ariola, 1899 to Czaplinski and Vaucher (1994); the nematode sub-family *Mastophorinae* Quentin, 1971 to Quentin (1971a, 1971b); the sucking lice family Enderleinellidae (Ewing, 1929) and the family Hoplopleuridae (Ewing, 1929) to Kim and Ludwig (1978); and, at the species level, to Kaneko (1954) and to Johnson (1959).

Because of unequal sample sizes, we compared differences in macroparasite prevalence between sexes using the Fisher exact test and we determined mean intensities using Mood's median test with Quantitative Parasitology 3.0 software (Rózsa et al., 2000; Reiczigel and Rózsa, 2005). We compared male and female host biometrics with Mann–Whitney's median test (Siegel and Castellan, 1988) in R 2.8.1 (R Development Core Team, 2008).

3. Results

We found two species of sucking lice in the Dadizele population of Pallas's squirrels (Table 1): 86 specimens (48 ♀, 32 ♂ and 6 nymphs) of *Hoplopleura erismata* (Johnson, 1959) on 14 hosts, and 45 specimens (18 ♀, 11 ♂ and 16 nymphs) of *Enderleinellus kumadai* (Kaneko, 1954) on 10 hosts. More male squirrels were infested by *H. erismata* ($P_{Fisher} = 0.01$) than females, without differences in lice burden between sexes ($P_{Mood} = 0.30$). Also, males harboured more *E. kumadai* ($P_{Mood} = 0.05$) than females, without differences in prevalence ($P_{Fisher} = 0.37$). Additionally, we found two immature females of a *Mastophorus* sp. nematode in the stomach lumen of one squirrel.

One species dominated the macroparasite fauna of the 29 Pallas's squirrel that we examined from the Antibes population (Table 1): 183 specimens of *E. kumadai* (113 ♀, 62 ♂ and 8 nymphs) were found on 16 hosts. More male squirrels were infected ($P_{Fisher} < 0.01$), with a larger number of sucking lice ($P_{Mood} = 0.03$), than females. We found a *Nosopsyllus fasciatus* (Bosc d'Antic, 1800) flea on two squirrels. We also found twelve incomplete and immature specimens of a *Hymenolepis* cestode (Weinland, 1858) in the small intestine of three squirrels from Villa Thuret.

We found no other macroparasites in the digestive tract, heart, lung, liver, kidneys, bladder, or body cavity of these 49 hosts.

Male and female Palla's squirrels from Dadizele and Cap d'Antibes had the same morphometry; Villa Thuret females were heavier than males ($P_{Mann-Whitney} = 0.01$; Table 1).

4. Discussion

Pallas's squirrels introduced into Japan carried at least 6 macroparasite species (Kaneko, 1954; Shinozaki et al., 2004; Asakawa, 2005; Sato et al., 2007): a hard tick, *Haemaphysalis flava*; two sucking lice, *E. kumadai* and *Neohaematopinus callosciuri*; a flea, *Ceratophyllus* (*Monopsyllus*) *anisus*; and three nematodes, *Brevistriata callosciuri*, *Strongyloides callosciureus* and *Gongylonema neoplasticum*. According to Shinozaki et al. (2004), only *H. flava* was native to Japan. In fact, there were no reports of *C.* (*M.*) *anisus* or of *N. callosciuri* in Japan before the Pallas's squirrel parasite fauna studies (Shinozaki et al., 2004; Asakawa, 2005; but see Beaucournu and Launay, 1990). *E. kumadai* was first described in 1954 by K. Kaneko from Pallas's squirrels originating from Taiwan and introduced into Japan on Izu-oshuzima Island in 1935. According to Sato et al. (2007), *S. callosciureus* would have been introduced with the founders. The stomach nematode *G. neoplasticum*, a parasite associated with Murinae, must have been acquired accidentally by the squirrel through the consumption of

Table 1
Morphology (mean ± SE) and macroparasite infestation characteristics for female and male Pallas's squirrels, *Callosciurus erythraeus*, in Belgium and France. Prevalence: P; mean intensity: mI; 95% confidence interval in brackets; the count range in parentheses.

Localities		Dadizele		Antibes	
Countries		Belgium		France	
Sex		Females	Males	Females	Males
Number of squirrels		11	9	16	13
Hosts					
Body mass (g)		312 ± 10 (251–369)	309 ± 6 (280–331)	366 ± 8 (310–430)	322 ± 15 (205–385)
Head-body (mm)		204 ± 4 (191–228)	208 ± 4 (198–230)	219 ± 2 (202–234)	215 ± 4 (182–237)
Tail (mm)		152 ± 3 (143–166)	148 ± 5 (124–167)	180 ± 2 (163–194)	174 ± 2 (156–187)
Hind foot (mm)		48 ± 1 (46–52)	48 ± 1 (47–50)	46 ± 1 (42–50)	45 ± 1 (41–50)
Arthropods					
Sucking lice					
Enderleinellus kumadai	P	31 [13–56]	67 [32–90]	31 [13–56]	85 [57–97]
	mI	(1; 1; 1; 1)	6 [1–16]	2 [1–3]	10 [4–24]
Hoplopleura erismata	P	46 [20–74]	100 [68–100]	0	0
	mI	3 [1–4]	8 [4–13]	–	–
Flea					
Nosopsyllus fasciatus	P	0	0	13 [2–37]	0
	mI	–	–	(1; 1)	–
Helminths					
Cestode					
Hymenolepis sp.	P	0	0	13 [2–37]	8 [<1–34]
	mI	–	–	(2; 4)	(6)
Nematode					
Mastophorus sp.	P	0	11 [1–44]	0	0
	mI	–	(2)	–	–

intermediary host insects (Anderson, 1992). Therefore, at least five species of macroparasites have been imported with Pallas's squirrels introduced into Japan since 1935. Four out of these five species are only found on Sciurids, and three of them (*N. callosciuri*, *B. callosciuri* and *E. kumadai*) are specialists of the Callosciurini tribe. The small number of macroparasite species found in France and Belgium may be related to fewer introduction events in these two countries and a low number of founders compared to Japan (see Oshida et al., 2007).

To our knowledge, the macroparasite fauna of Pallas's squirrels on their native area has not been documented (Shinozaki et al., 2004; but see Durden and Musser, 1994a, 1994b). The endoparasite fauna for other *Callosciurus* squirrels consists of few species, which was attributed to tree-canopy use behaviour (Dunn et al., 1968). This behaviour, as well as the scarcity of other rodent species cohabiting in the areas studied in Belgium and France, may explain the very low number of accidental parasitism observed on introduced Pallas's squirrel. For example, the macroparasites identified from another Sciurid introduced into France, the Siberian chipmunk, *Tamias* (*Eutamias*) *sibiricus barberi* Johnson et Jones, 1955 (see Obolenskaya et al., 2009), represent 19 taxa observed in four populations (Vourc'h et al., 2007; Pisanu et al., 2007, 2008, 2009; Beaucournu et al., 2008), three of which were imported, three newly hosted (a flea, a hard tick, and a nematode) and 13 acquired accidentally. Chipmunks are ground-dwelling squirrels that live in burrows and spend less time in the tree-canopy (Chapuis, 2005); this behaviour may increase the probability of acquiring infective stages of parasites available in the environment, even in urbanised localities.

Pallas's squirrels in Belgium were observed to have only one accidental acquisition. We could not identify the two immature female nematodes to species level; however, in Europe, only one species of the genus *Mastophorus* is known to infect a great number of rodent hosts primarily belonging to the superfamily Muroidea: *M. muris* (Gmelin, 1790). This species has an indirect life-cycle, and infective stages must first develop in an intermediate terrestrial insect host (Anderson, 1992). In France, only two accidental acquisitions were detected. *N. fasciatus*, also known as the rat's flea, has a very large host spectrum, but primary hosts are in the genus *Rattus* (Beaucournu and Launay, 1990). Collectively, these results indicate that Pallas's squirrels may accidentally acquire a few parasites from co-inhabiting with native Muroid rodents, probably rats (*Rattus* spp.). This finding agrees with Shinozaki et al. (2004), who found the flea, *C.* (*M.*) *anisus*, a common rat flea in East Asia (Beaucournu and Launay, 1990).

We found sex-biased sucking lice infestations. This result agrees with other studies that show higher ectoparasite infestations are observed on male rodents (Randolph, 1975; Poulin, 1996; Perkins et al., 2003) including sucking lice on squirrels (Durden, 1980). We did not find sexually dimorphic body size in Pallas's squirrels (see also: Cassini and Guichón, 2009). Therefore, any differences in ectoparasite infestations between sexes, as already documented in non-sexually dimorphic mammals (Moore and Wilson, 2002; Wilson et al., 2002), may have been caused by differences in genetics (Coltman et al., 2001), physiol-

ogy (Perez-Orella and Schulte-Hostedde, 2005), immunity (Hughes and Randolph, 2001), or behaviour-related exploration and space use (Boyer et al., 2010).

As expected, the macroparasite species richness we found in the populations of Pallas's squirrels established in Europe was very low and consisted mainly of specialists imported from Asia (Durden and Musser, 1994a, 1994b). This result is consistent with the pattern of low diversity of macroparasites in introduced hosts (Torchin et al., 2003), as it is for introduced squirrels (López-Darias et al., 2008). The lack of accidental or newly acquired parasites is likely due to the low number of mammalian species present in urbanised areas. We conclude that the risks of infestation by ectoparasites shared by Pallas's squirrels and native species, almost exclusively red squirrels and humans, are minimal in urban parks in France and Belgium. Additionally, in Belgium, the population of Pallas's squirrels has probably been eradicated due to an early eradication measure in 2008 (Stuyck, 2009). Such management actions prevent increased sanitary risks that may arise if introduced populations were allowed to spread to areas where there is increased parasite exposure (see Beugnet and Marié, 2009).

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References

Anderson, R.C., 1992. Nematodes Parasites of Vertebrates, their Development and Transmission. CAB International, Wallingford, UK, 578 pp.

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

Beaucournu, J.-C., Launay, H., 1990. Les puces de France et du bassin méditerranéen occidental. Faune de France 76. Fédération Française des Sociétés de Sciences Naturelles, Paris, France, 548 pp.

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.

Berry, R.J., 1970. The natural history of the house mouse. Field Stud. 3, 219–262.

Beugnet, F., Marié, J.-L., 2009. Emerging arthropod-borne diseases of companion animals in Europe. Vet. Parasitol. 163, 298–305.

Bordes, F., Langand, J., Feliu, C., Morand, S., 2007. Helminth communities of an introduced hare (*Lepus granatensis*) and a native hare (*Lepus europaeus*) in Southern France. J. Wildlife Dis. 43, 747–751.

Boyer, N., Réale, D., Marmet, J., Pisanu, B., Chapuis, J.-L., 2010. Personality, space use, and tick load in an introduced population of Siberian chipmunk, *Tamias sibiricus*. J. Anim. Ecol. 79, 538–547.

Cassini, G.H., Guichón, M.L., 2009. Variaciones morfológicas y diagnosis de la ardilla de vientre rojo, *Callosciurus erythraeus* (Pallas, 1779), en Argentina. Mastozool. Neotrop. 16, 39–48.

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.

Coltman, D.W., Pilkington, J., Bruuk, L.E.B., Wilson, K., Pemberton, J.M., 2001. Positive genetic correlation between parasite resistance and body size in a free-living ungulate population. Evolution 55, 2116–2125.

Craine, N.G., Randolph, S.E., Nuttall, P.A., 1995. Seasonal variation in the role of grey squirrels as hosts of *Ixodes ricinus*, the tick vector of the Lyme disease spirochaete, in a British woodland. Folia Parasitol. 42, 73–80.

Czaplinski, B., Vaucher, C., 1994. Family Hymenolepididae Ariola, 1899. In: Khalil, L.F., Jones, A., Bray, R.A. (Eds.), Keys to the Cestodes Parasites of Vertebrates. CAB International, Wallington, UK, pp. 595–663.

Dijkstra, V., Overman, W., Verbeylen, G., 2009. Inventarisatie Pallas' eekhoorn bij Weert. Zoogdiervereniging rapport 2009.21, Zoogdiervereniging, Arnhem, Nederland (in Dutch, with English abstract).

Duckworth, J.W., Timmins, R.J., Molur, S., 2008. *Callosciurus erythraeus*. In: IUCN 2010. IUCN Red List of Threatened Species. Version 2010.1. www.iucnredlist.org.

Dunn, F.L., Lim, B.L., Yap, L.F., 1968. Endoparasite patterns in mammals of the Malayan rain forest. Ecology 49, 1179–1184.

Durden, L.A., 1980. Seasonal abundance of fleas (Siphonaptera) and sucking lice (Anoplura) on gray squirrels, *Sciurus carolinensis*, in central Tennessee, USA. J. Med. Entomol. 17, 483–484.

Durden, L.A., Musser, G.G., 1994a. The sucking lice (Insecta, Anoplura) of the world: a taxonomic checklist with records of mammalian hosts and geographical distribution. Bull. Am. Mus. Nat. Hist. 218, 1–90.

Durden, L.A., Musser, G.G., 1994b. The mammalian hosts of the sucking lice (Anoplura) of the world: a host–parasite List. Bull. Soc. Vector Ecol. 19, 130–168.

Gerriet, O., 2009. Répartition de l'écureuil à ventre rouge *Callosciurus erythraeus* (Pallas, 1779) (*Rodentia, Sciuridae*) dans les Alpes-Maritimes (France). Biocosme Mésogéen (Nice) 26, 139–148.

Hasegawa, H., Sato, H., Iwakiri, E., Ikeda, Y., Une, Y., 2008. Helminths collected from imported pet Murids, with special reference to concomitant infection in the golden hamsters with three pinworm species of the genus *Syphacia* (Nematoda: Oxyuridae). J. Parasitol. 94, 752–754.

Hughes, V.L., Randolph, S.E., 2001. Testosterone depresses innate and acquired resistance to ticks in natural rodent hosts: a force for aggregated distribution of parasites. J. Parasitol. 87, 49–54.

Ide, Y., Inaba, T., Asakawa, M., 2000. Prevalence of the parasitic helminths in pet animals belonging to orders Marsupialia and Edentata. Jpn. J. Zool. Wildlife Med. 5, 157–162 (in Japanese, with English abstract).

Irwin, P.J., 2002. Companion animal parasitology: a clinical perspective. Int. J. Parasitol. 32, 581–593.

Johnson, P.T., 1959. The rodent-infesting Anoplura (Sucking lice) of Thailand, with remarks on some related species. Proc. U.S. Nat. Mus. 110, 569–598.

Jouanin, C., 1986. Une espèce inattendue pour la faune française: un écureuil asiatique acclimaté sur le Cap d'Antibes. Rev. Ecol. (Terre Vie) 41, 107–109.

Jouanin, C. 1992. L'écureuil à ventre rouge d'Antibes. In: Sénotier J.-L. (Ed.) Introductions et réintroductions de mammifères sauvages, XIVème colloque de la S.F.E.P.M., Orléans, 20–21 octobre 1990, Nature Centre, Orléans, France, pp. 277–284.

Kaneko, K., 1954. Description of a new species of *Enderleinellus* collected from the South Formosa squirrel naturalized into Japan. Bull. Tokyo Med. Dent. Univ. 1, 49–52.

Kim, K.C., Ludwig, H.W., 1978. The Family classification of the Anoplura. Syst. Entomol. 3, 249–284.

López-Darias, M., Ribas, A., Feliú, C., 2008. Helminth parasites in native and invasive mammal populations: comparative study on the Barbary ground squirrel *Atlantoxerus getulus* L. (Rodentia, Sciuridae) in Morocco and the Canary Islands. Acta Parasitol. 53, 296–301.

Moore, S.L., Wilson, K., 2002. Parasites as a viability cost of sexual selection in natural populations of mammals. Science 297, 2015–2018.

Obolenskaya, E.V., Lee, M.-Y., Dokuchaev, N.E., Oshida, T., Lee, M.-S., Lee, H., Lissovsky, A.A., 2009. Diversity of paleartic chipmunks (*Tamias*, Sciuridae). Mammalia 73, 281–298.

Oshida, T., Torii, H., Lin, L.-K., Lee, J.-K., Chen, Y.-J., Endo, H., Sasaki, M., 2007. A preliminary study of *Callosciurus* squirrels introduced into Japan. Mamm. Study 32, 75–82.

Perez-Orella, C., Schulte-Hostedde, A.I., 2005. Effect of sex and body size on ectoparasite loads in the northern flying squirrel (*Glaucomys sabrinus*). Can. J. Zool. 83, 1381–1385.

Perkins, S.E., Cattadori, I.M., Tagliapietra, V., Rizzoli, A.P., Hudson, P.J., 2003. Empirical evidence for key hosts in persistence of a tick-borne disease. Int. J. Parasitol. 33, 909–917.

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., Lebailleux, L., Chapuis, J.-L., 2009. Why do Siberian chipmunks *Tamias sibiricus* (Sciuridae) introduced in French forests acquired so few intestinal nematode species from native sympatric Murids? Parasitol. Res. 104, 709–714.

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.

Pisanu, B., Marsot, M., Marmet, J., Chapuis, J.-L., Réale, D., Vourc'h, G., 2010. Introduced Siberian chipmunks are more heavily infested by ixodid ticks than are native bank voles in a suburban forest in France, Int. J. Parasitol., doi:10.1016/j.ijpara.2010.03.012.

Poulin, R., 1996. Sexual inequalities in helminth infections: a cost of being a male? Am. Nat. 147, 287–295.

Quentin, J.-C., 1971a. Morphogenèse larvaire du Spiruride *Mastophorus muris* (Gmelin, 1790). Ann. Parasitol. Hum. Comp. 45, 839–855.

Quentin, J.-C., 1971b. Sur les modalités d'évolution chez quelques lignées d'helminthes de rongeurs Muroidea. Cah. O.R.S.T.O.M. sér. Ent. méd. Parasitol. 9, 103–176.

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

R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org.

Randolph, S.E., 1975. Patterns of distribution of the tick *Ixodes trianguliceps* Birula on its hosts. J. Anim. Ecol. 44, 451–474.

Rózsa, L., Reiczigel, J., Majoros, G., 2000. Quantifying parasites in samples of hosts. J. Parasitol. 86, 228–232.

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.

Shinozaki, Y., Shiibashi, T., Yoshizawa, K., Murata, K., Kimura, J., Maruyama, S., Hayama, Y., Yoshida, H., Nogami, S., 2004. Ectoparasites of the Pallas squirrel. *Callosciurus erythraeus*, introduced to Japan. Med. Vet. Entomol. 18, 61–63.

Siegel, S., Castellan Jr., N.J., 1988. Non-Parametric Statistics for the Behavioral Sciences. MacGraw Hill Inc., Singapore, 399 pp.

Smith, K.F., Carpenter, S.M., 2006. Potential spread of introduced black rat (*Rattus rattus*) parasites to endemic deer mice (*Peromyscus maniculatus*) on the California Channel Islands. Divers. Distrib. 12, 742–748.

Stuyck, J., 2009. Pallas's squirrel *Callosciurus erythraeus* introduced in Belgium. In: 7th European Vertebrate Pest Management Conference, National veterinary school of Lyon, Marcy l'Etoile, France, 8–12 September 2009 (English summary).

Tompkins, D.M., Poulin, R., 2006. Parasites and biological invasions. In: Allen, R.B., Lee, W.G. (Eds.), Biological Invasions in New Zealand. Ecological Studies, vol. 186. Springer-Verlag, Berlin, Heidelberg, pp. 67–84.

Torchin, M.E., Lafferty, K.D., Dobson, A.P., McKenzie, V.J., Kuris, A.M., 2003. Introduced species and their missing parasites. Nature 421, 628–630.

Torchin, M.E., Mitchell, C.E., 2004. Parasites, pathogens, and invasions by plants and animals. Front. Ecol. Environ. 2, 183–190.

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.

Wilson, K., Bjørnstad, O.N., Dobson, A.P., Merler, S., Poglayen, G., Randolph, S.E., Read, A.F., Skorping, A., 2002. Heterogeneities in macroparasite infections: patterns and processes. In: Hudson, P.J., Rizzoli, A., Grenfell, B.T., Heesterbeek, H., Dobson, A.P. (Eds.), The Ecology of Wildlife Diseases. Oxford University Press, Oxford, UK, pp. 6–44.

Yokoyama, Y., Inaba, T., Asakawa, M., 2003. Preliminary report on prevalence of the parasitic helminths obtained from pet primates transported into Japan. Jpn. J. Zool. Wildlife Med. 8, 83–93 (in Japanese, with English abstract).