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ORIGINAL PAPER

Parasites of wild rabbits (*Oryctolagus cuniculus*) from an urban area in Germany, in relation to worldwide results

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Abstract The European rabbit (*Oryctolagus cuniculus*) belongs to the most invasive and successful mammalian species, which is distributed nearly worldwide. In Europe, they inhabit broad parts of the mainland and subsequently reached several European islands via anthropogenic diversion. Rabbits can also serve as hosts for numerous parasite species. The parasite and pathogen fauna of *O. cuniculus* have been well documented in various European countries, although studies in Germany are scarce. Until now, a comprehensive survey combining recent international studies over parasite fauna of wild rabbits had not been conducted. We examined 50 wild rabbits from an urban area near Aachen (Germany) to identify their metazoan parasite fauna, and then compared our findings to previous international investigations. A total of nine parasite species were isolated consisting of four endoparasite species (*Cittotaenia denticulata*, *Graphidium strigosum*, *Passalurus ambiguus*, and *Trichostrongylus retortaeformis*) and five ectoparasite species (*Cheyletiella parasitivorax*, *Ixodes ricinus*, *Leporacarus gibbus*, *Haemodipsus ventricosus*, and *Spilopsyllus cuniculi*). Among the ectoparasites were two verifiable human pathogenic species and two potentially pathogenic species. In comparison to previous studies, a high number of similarities in composition of helminth species fauna were revealed. Furthermore, our results showed partial agreement with international surveys in prevalence and mean intensity of the parasites *C. denticulata*, *G. strigosum*, *P. ambiguus*, and *T. retortaeformis*.

Introduction

The European rabbit (*Oryctolagus cuniculus*) belongs to the family Leporidae and is distributed worldwide. In Europe, it is one of the most popular game animals (Palomares 2001). Furthermore, varieties of this species are commercially raised for meat, skin, and wool and play an important role as pets (Lebas et al. 1997). Rabbits are also used extensively in medical research as well as for chemical and consumer product safety testing. Oldest palaeontological finds of *O. cuniculus* are approximately 6.5 million years old and were discovered in south of Spain, Andalusia (Monnerot et al. 1994). The introduction of rabbits into Germany most likely took place in the twelfth century (Gebhardt 1996). During the age of exploration, rabbits were left on hundreds of islands as a food source for later voyages, often with devastating consequences for island ecologies (North et al. 1994). While the general rate of expansion of rabbits is approximately 54 km/year, the rate of expansion in Europe reaches up to 200 km/year (Flux and Fullagar 2008). Considering the natural migration behavior and human-caused diversion, wild rabbits were able to spread almost worldwide and

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integrated themselves as invasive species into many ecological systems (Flux and Fullagar 2008; Fenner 2010). Subsequently, they had, and still have, a massive impact on native flora and fauna (Jaksic et al. 1979; North et al. 1994). The habitat of the European rabbit includes open areas with soft and sandy soil, which allows it to build burrows (Kolb 1985). They accept a wide range of soil conditions, even if close to human inhabited areas. Rabbits are also so successful in building their burrows that they are often considered a pest species (Trout et al. 1986; Kolb 1994).

Wild rabbits are a mammalian species which inhabit successful, anthropogenically formed areas, such as cemeteries, gardens, or parks. Worldwide distribution and success of wild rabbits are inseparably linked to human activities (Parker 1990; Fenner 2010).

Rabbits inhabit large, complex, self-built burrow systems (Bravo et al. 2009). The burrowing activity can heavily impact other organisms inhabiting the same ecosystem. Their grazing activity can also affect plant composition, by avoiding or preferring special food plants in a determined habitat. Conversely, they serve as prey for at least 29 mammalian and avian predator species (Delibes-Mateos et al. 2008; Garcia-Bocanegra et al. 2010). Thus, European rabbits may be characterized as a keystone species in ecosystems (Delibes-Mateos et al. 2008).

The (metazoan and protozoan) parasite and pathogen fauna of *O. cuniculus* has been well documented in various countries of Europe (e.g., Boag 1988; Allan et al. 1999; Molina et al. 1999; Foronda et al. 2003b; Lello et al. 2004; Eira et al. 2007), whereas studies in Germany are scarce (e.g., Haupt and Hartung 1984; Sibila 2008; Starkloff 2009). Thus far, Digenea (8 species), Cestoda (14), Nematoda (43), Acarina (15), Diptera (8), Phthiraptera and Siphonaptera (7), and Pentastomida (1) have been identified to parasitize wild rabbits (as intermediate and final hosts) worldwide or were successfully infected experimentally (e.g., Shepherd and Edmonds 1972; Tenquist and Charleston 1980; Boag 1988; Audebert and Durette-Desset 2007; Eira et al. 2007). Further several protozoan parasites of wild and domestic rabbits are known, e.g., *Eimeria intestinalis* (Sporozoa) (Coudert et al. 1993), *Eimeria coecicola* (Al-Quraishy et al. 2012), *Sarcocystis cuniculi* (Sporozoa) (Munday et al. 1980), and *Trypanosoma nabiasi* (Flagellata) (Mohamed and Molyneux 1987). Among the protozoan rabbit parasites are several human pathogenic species like the microsporidian *Encephalitozoon cuniculi* (Mathis et al. 1996), the cryptosporidian *Cryptosporidium cuniculus* (Hadfield and Chalmers 2012) and *Toxoplasma gondii* (Sporozoa) (Sroka et al. 2003). The aim of the present study was to document the scarcely studied metazoan parasite fauna of wild rabbits (*O. cuniculus*), to clarify their potential as reservoir hosts of zoonotic parasites, and to compare our results (from an urban region) with preceding international studies.

Materials and methods

A total of 50 wild rabbits (25 males/25 females) (*O. cuniculus*) were hunted by a licensed hunter in Eschweiler (Germany), a small city close to Aachen. All rabbits were collected from the same area, close to human dwellings. Sampling was conducted during the months of October and November, 2009. Immediately after a rabbit was shot, it was deep frozen to −20 °C. Prior to examination, each rabbit was defrosted at room temperature. The biometric data, total weight (in grams), total length (in centimeters), and sex were then subsequently recorded. Statistical tests were performed using GraphPad Prism version 5.01. Total length and weight were tested for normal distribution using the D'Agostino and Pearson omnibus K2 normality test (GraphPad Prism). Following the recording of this data, ears, coats, skin, nostrils, and perianal regions were examined for ectoparasites (e.g., lice, ticks, and fleas). Ectoparasites were abstracted using fine forceps and then stored in ethanol (70 %). The body cavities were opened, and the alimentary tracts were removed for further examinations. All organs were separated from the surrounding fat tissue and placed in Petri dishes containing physiological saline solution. The organs were then examined for endoparasites under a dissection stereomicroscope. Weights of abdominal organs, lungs, and heart were recorded. Endoparasites were isolated with fine forceps. The weights of intestinal organs were then also recorded. Organs composing the digestive track were examined and also checked for degree of nutrition. Isolated parasites were fixed in 4 % borax-buffered formalin and preserved in solution of 70 % ethanol/5 % glycerin. For identification purposes, nematodes were dehydrated in a graded ethanol series and transferred to 100 % glycerin (Riemann 1988). Cestodes were stained with acetic carmine, dehydrated, cleared with eugenol or creosote, and then mounted in Canada balsam. For species determination, all ectoparasites were cleared with 10 % potassium hydroxide solution for over 12 h, dehydrated, and then mounted in Canada balsam. Literature for helminth parasite identification included original descriptions, as well as papers of Khalil et al. (1994) regarding Cestoda and those of Sprehn (1961), Anderson et al. (1974), and Audebert et al. (2000) for Nematoda. The insect species identification was based on the descriptions of Peus (1953) and Weidner and Sellenschlo (2010). Arachnid species were identified using the publications of Karg (1971), Smith (1973), Volgin (1987), Lane and Crosskey (1993), and Harrison and Foelix (1999). The parasitological terms (prevalence, mean intensity, intensity, and mean abundance) followed the recommendations of Bush et al. (1997). For comparison of previous parasitological investigations (endo- or ectoparasites), the following studies were included in our analysis: Bull (1959): New Zealand, *n* rabbits=727 and years of sampling, 1953–1956 and 1958–1959); Boag (1988):

Eastern Scotland, *n* rabbits=985 and years of sampling, 1977–1986 (statistical analyses were done using the SPSS program, Boag 1988). Allan et al. (1999): North Yorkshire, England, *n* rabbits=95 and years of sampling, 1992–1996. Rabbits were caught monthly. Prevalence of each species was analyzed using a logistic model with year, sex, year×sex interaction, and weight as independent variables. Worm burdens were analyzed using a generalized linear model with an over-dispersed Poisson distribution (Allan et al. 1999). Additionally, a quadratic weight term was fitted to test for nonlinearity of the relationship between worm burden and weight. Molina et al. (1999) (Navarra, Spain, *n* rabbits=167 and years of sampling, 1994–1995) compared prevalences and mean intensities using ×2 and the Mann–Whitney *U* test, respectively. The correlation between host weight and the intensity of infection for different species was tested using the Spearman rank correlation test (Molina et al. 1999). Foronda et al. (2003a) (Tenerife, Canary Islands, *n* rabbits 104 and years of sampling, 1998–2000) used Statistical ×2 and ANOVA tests to determine differences in the prevalence and mean intensities of helminth species. Helminth counts were logarithmically transformed to normalize the distribution. According to Foronda et al. (2003b) (Azores, Atlantic ocean, *n* rabbits 89 and years of sampling, 1995–1996 and Madeira, Atlantic ocean, *n* rabbits 24 and years of sampling, 1996), Chi-square tests were used to evaluate the differences in prevalence (Bush et al. 1997) between the collecting points. Eira et al. (2007) (Dunas de Mira, Portugal, *n* rabbits 163 and years of sampling, 2000–2004) tested differences in helminth prevalence according to year and sex using Chi-square analysis, followed by Fisher's exact test (two sided) for pairwise comparisons.

Results

Biometric data and parasite diversity

The adult rabbits were examined, and results showed a mean total weight of 1,430.3 g (ranging from 707.4 to 1942.5 g; standard deviation (SD), 202.1 g) and mean total length of 33.2 cm (ranging from 27.1 to 39.8 cm; SD, 2.314 cm). Mean total length and weight of males and females did not differ significantly (Mann–Whitney unpaired two-tailed *U* test; $P<0.05$) (using GraphPad Prism Software 5,01). During the parasitological investigations, 92,770 parasite specimens were identified, belonging to nine parasite species. The parasitic fauna consisted of four endo- and five ectoparasite species (Table 1). Each rabbit was infected with a range of 1 to 4 (mean, 3.26) endoparasite species and 1 to 5 (mean, 2.66) ectoparasite species. The nematode *Graphidium strigosum* (Fig. 1) was obtained from the stomach, while the nematodes *Trichostrongylus retortaeformis* and *Passalurus ambiguus* and the cestode *Cittotaenia denticulata* (Figs. 2–4) were isolated from the digestive tract. The nematode *T. retortaeformis* was isolated from both the duodenum and the upper part of the jejunum, respectively, whereas *C. denticulata* was limited to the jejunum (Figs. 3, 4). *P. ambiguus* could also be found in the caecum, as well as in the proximal part of the colon. The tick *Ixodes ricinus* (Fig. 5), the louse *Haemodipsus ventricosus* (Fig. 6), and the flea species *Spilopsyllus cuniculi* (Fig. 7) were partly directly visible and found in the fur, with the first two mentioned species additionally on the skin of the inner ear conch. The ectoparsitic mites *Leporacarus gibbus* (Fig. 8) and *Cheyletiella parasitivorax* (Figs. 9, 10) were exclusively found in the fur. The parasite fauna included the human pathogenic species *I. ricinus* (Fig. 5) and *C. parasitivorax* (Figs. 9, 10) and two other potentially human pathogenic species: *Spilopsyllus cuniculi* (Fig. 7) and *Leporacarus gibbus* (Fig. 8) (Beck and Clark 1997; Beck and Pfister 2006; Olsen and Roth 1947; Rosen 2011).

Discussion

Parasite comparison with previous studies

For our comparative analysis, the following data sets of the endoparasite fauna of *O. cuniculus* were used: Bull (1959), Boag (1988), Allan et al. (1999), Molina et al. (1999), Foronda et al. (2003a, b), and Eira et al. (2007). In these studies, a total of 16 metazoan parasite species were found, consisting of Digenea (*Fasciola hepatica*), Cestoda (*Andrya cuniculi*, *Cittotaenia ctenoides*, *C. denticulata*, *Ctenosaura pectinata*, *Leporidotaenia wimerosa*, *Taenia serialis*, and *Taenia pisiformis*) and Nematoda (*Dermatoxys hispaniensis*, *Gongylonema neoplasticum*, *G. strigosum*, *Nematodiroides zembrae*, *Nematodirus battus*, *P. ambiguus*, *T. retortaeformis*, *Trichuris leporis*). In the present study, the infestation rates of *C. denticulata* and *G. strigosum* were high (see Figs. 11 and 12) when compared with other parasitological investigations. In previous studies, the relatively high intensity of 22,739 specimens of *P. ambiguus* in a single rabbit as seen here (Table 1) has not been observed.

Parasite fauna of wild rabbits in Germany

Data on the protozoan and metazoan parasite fauna of wild rabbits (*O. cuniculus*) are scarce in Germany. For this reason, the present study was conducted in Germany to evaluate the health status of native rabbits in this region. Nine metazoan parasite species were isolated, including five ectoparasite and four endoparasite species. The rabbits were not checked for protozoan parasite species. All nine isolated parasite species are common in *O. cuniculus*. *Leporacarus gibbus* (formerly

Table 1 Results of rabbit examination from collecting area Eschweiler (Germany)

Species	*P*	*A*	*I*	mI	Total size	
					Min–max	Mean
Cestoda						
Cittotaenia denticulata	88.0	8.0	1–121	9.1	2.12–40.00 cm	28.26 cm
Nematoda						
Graphidium strigosum	98.0	117.4	1–754	119.8	♀♀, 14.41–18.96 mm	♀♀, 17.16 mm
					♂♂, 10.14–14.12 mm	♂♂, 13.37 mm
Trichostrongylus retortaeformis	72.0	332.3	1–11597	461.6	♀♀, 7.27–9.18 mm	♀♀, 8.42 mm
					♂♂, 6.34–8.45 mm	♂♂, 7.96 mm
Passalurus ambiguus	68.0	1247.1	1–22739	1834.0	♀♀, 8.32–11.00 mm	♀♀, 10.6 mm
					♂♂, 4.26–4.97 mm	♂♂, 4.80 mm
Acarina						
Cheyletiella parasitivorax[b]	40.0	1.6	1–16	4.0	♀♀/♂♂, 0.36–0.38 mm	♀♀/♂♂, 0.37 mm
Ixodes ricinus[a]	16.0	0.1	1–2	1.1	♀♀/♂♂, 4.03–4.35 mm	♀♀/♂♂, 4.10 mm
Leporacarus gibbus[c]	98.0	135.5	1–413	138.3	♀♀, 0.51–0.54 mm	♀♀, 0.53 mm
					♂♂, 0.40–0.43 mm	♂♂, 0.42 mm
Insecta						
Spilopsyllus cuniculi[b]	86.0	10.8	1–45	12.5	♀♀, 1.82–2.14 mm	♀♀, 1.98 mm
					♂♂, 1.45–1.56 mm	♂♂, 1.54 mm
Haemodipsus ventricosus	32.0	2.2	1–28	7.1	♀♀, 1.29–1.35 mm	♀♀, 1.33 mm
					♂♂, 1.05–1.20 mm	♂♂, 1.12 mm

A abundance, *I* intensity, *mI* mean intensity, *P* prevalence

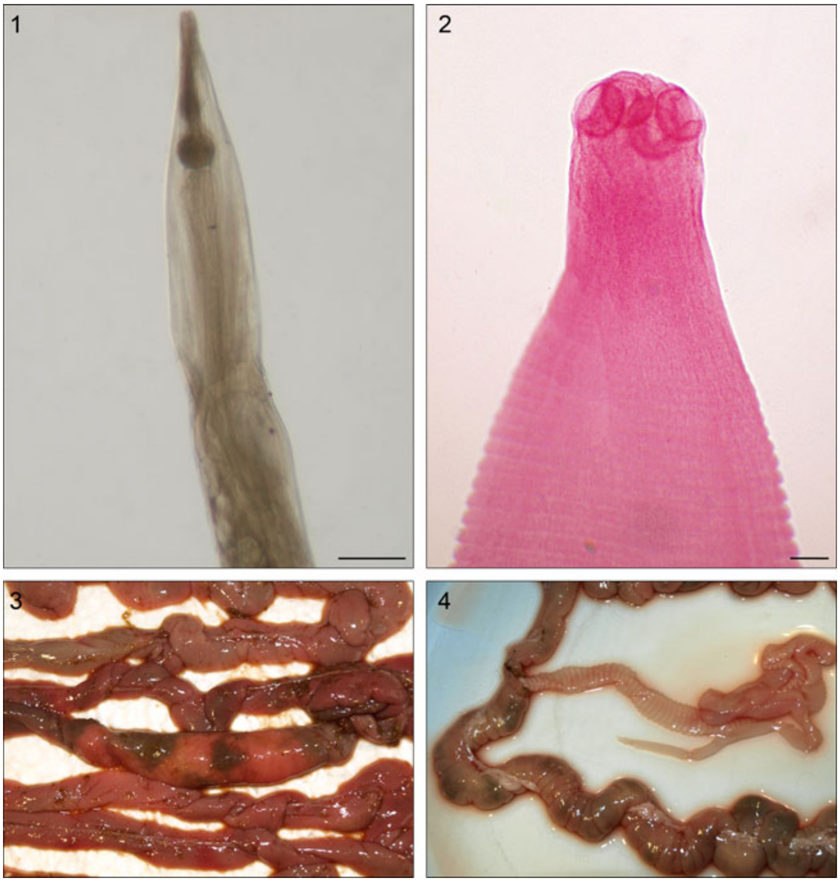
[a] Verifiable human pathogenic parasites

[b] Human pathogenic but rarely

[c] Potentially human pathogenic

Listrophorus gibbus) is a rabbit fur mite that is rarely found on laboratory rabbits but frequently on wild rabbits and hares (*Lepus europaeus*) (Niekrasz et al. 1998). This mite does little harm to the host and therefore does not cause significant diseases (Niekrasz et al. 1998). On rare occurrence, humans can be parasitized, and have been in the past, because of close contact with the primary hosts, such as pet rabbits (Burns 1987). The life cycle of this obligate parasite has not yet been fully described; however, it is known that all general life stages (including adults and two nymphal stages) occur on the rabbits (Birke et al. 2009). *C. parasitivorax* is a much more virulent mite species, which has a direct, host-to-host pathway of transmission via body contact. This mite is not host specific and is therefore able to infest other animals, such as humans (Beck and Pantchev 2006). The female mites lay their eggs close to the skin of the hair, and under optimal conditions, they have a 5-week life cycle (Praag van E et al. 2010). The mite *C. parasitivorax* is a facultative parasite, feeding on other fur mites or parasitizing mammalian hosts in cases where the immune system is weak (Medeiros 2012).

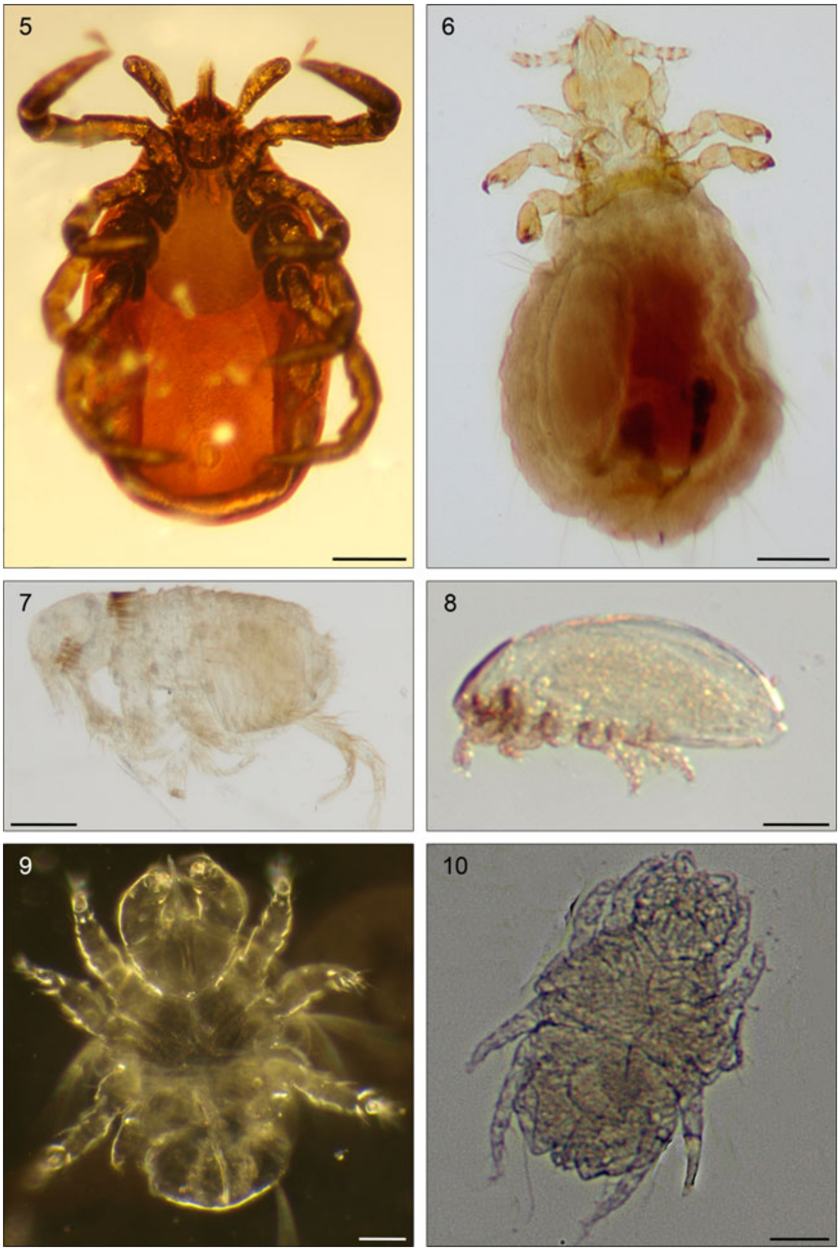
The tick species *I. ricinus* shows a wide range of hosts in regions of Western Europe and Northern Africa (Mejlon 2000). This tick acts as vector for several important zoonotic pathogens, e.g., *Borrelia burgdorferi* s.l. (spirochaetes) and tick-borne encephalitis virus (Floris et al. 2006). Preferred habitats are woodlands and forests, whereby a humidity of more than 80 % in the microclimate is needed for survival (Piesman and Gern 2004). The stages of *I. ricinus* infest a remarkably wide range of hosts including birds, reptiles, and mammals (Bauwens et al. 2006). Climate warming is predicted to have a major impact on the further distribution of *I. ricinus* throughout areas with moderate climate, such as Scandinavia or Eastern Europe (Jaenson and Lindgren 2010). Reasons for the predicted scenario are based on the tight ecological complexity between natural and invasive plant species and hosts, which will further spread and, in turn, will enable *I. ricinus* and associated pathogens to spread, too. The flea *Spilopsyllus cuniculi* is a common parasite of European rabbits (Praag van E et al. 2010). Its reproductive cycle is tightly synchronized to the reproductive cycle of the European rabbit (Biebel 2007). Rising estrogen and corticosteroid levels at the end of the host pregnancy induce flea reproduction, which lay their eggs close to roost. Hatched flea larvae ingest feces of adult fleas containing dried



Figs. 1-4 Endoparasites. **1** *G. strigosum*. Anterior end. Light micrograph. *Scale bar*, 670 μm. **2**–**4** *C. denticulata*. **2** Anterior end. Light micrograph. *Scale bar*, 2.4 mm. **3** Natural localization in host (small intestine). Folded alignment (*light area in center*), gut is swollen for several times (note adjacent gut). Picture illustrates impairment of digestion. **4** *C. denticulata* particularly leaked from small intestine, observed during examination. Picture display space-demanding process of cestode infection

blood. The flea is the main vector of myxomatosis and may transmit *Francisella tularensis*, which causes tularemia (Wiegand 2007). The myxomatosis virus was previously used to control rabbit populations in France and Australia (Barcena et al. 2000), however, all efforts failed.

H. ventricosus is the only identified louse species in this study, showing comparably low values of prevalence and intensity. Sucking lice are permanent, hematophagous, ectoparasitic insects of mammals found throughout the world with approximately 550 described species (Durden and Rausch 2007). Despite the small number of identified species, the genus includes seven described species, which represent a wide geographical distribution. *Haemodipsus africanus* occurs in Southern Africa, *Haemodipsus brachylagi* in Western North America, *Haemodipsus conformalis* in Central Asia, *Haemodipsus leporis* and *Haemodipsus lyriocephalus* in Eurasia, *Haemodipsus setoni* in North America, and *H. ventricosus* in Europe (Durden and Musser 1994). Furthermore, some of these louse species have been introduced into other bio-geographical regions and ecosystems. For example, *H. ventricosus* is a typical louse of the domestic rabbit and has been introduced, along with its host, around the world, so that it now lives virtually as a cosmopolitan (Kim et al. 1986; Durden and Musser 1994). Due to prevalences of at least 40 % for the three ectoparasitic species *C. parasitivorax*, *Leporacarus gibbus* and *Spilopsyllus cuniculi,* they can be characterized as an eudominant species. Furthermore, the latter two species showed prevalence rates of at least 86 % and can thus be characterized as core species. On account of the close physiological adaptation of *Spilopsyllus cuniculi* to wild rabbits and their prevalence rates, both species exhibit a high degree of parasite–host adaptation. In addition, both species are hematophagous, and therefore it can be assumed that they are harmful to wild rabbits. Given the accessory predacious lifestyle of *C. parasitivorax,* the damages done to rabbits still have to be clarified (Medeiros 2012). The only cestode species identified here, *C. denticulata,* has a well-described life cycle. Eggs are transported within proglottides through rabbit feces. The infectious larval stages develop inside the eggs, which must be ingested by an oribatid mite to start further development (Boag et al. 2001). Inside the intermediate host, the tapeworm develops to an infectious cysticercoid stage. If the final host ingests the mite with food, *C. denticulata* matures to an adult stage and completes its life cycle (Boag et al. 2001). The intermediate hosts (oribatid mites) are the dominant component of the microarthropod fauna in most forest floor, grassland, or desert ecosystems (Seastedt 1984). Considering the fact that these mites often comprise more than 50 % of the total microarthropod fauna



Figs. 5–10 Ectoparasites. **5** *I. ricinus*. Female. Ventral. Light micrograph. *Scale bar*, 1.15 cm. **6** *H. ventricosus*. Gravide female. Light micrograph. *Scale bar*, 300 µm. **7** *Spilopsyllus cuniculi*. Mazerated. Light micrograph. *Scale bar*, 450 µm. **8** *Leporacarus gibbus.* Female. Light micrograph. *Scale bar*, 130 µm. **9** *C. parasitivorax*. Ventral. Light micrograph. *Scale bar*, 70 µm. **10** *C. parasitivorax*. Dorsal. Light micrograph. *Scale bar*, 100 µm

(Seastedt 1984), the transmission to rabbits is rather easy. Adult *C. denticulata* demands plenty of space inside of the small intestine (Figs. 3, 4) of the host. Considering the size of this tapeworm (Fig. 4), it is assumed that the parasite causes two main implications: blocking of intake of nutrition and intestinal obstruction (Fig. 4). Furthermore, loss of nutrients is assumed. In addition, adult *C. denticulata* were generally arranged in the intestine with older proglottides pressed against younger proglottides (Fig. 3), thus aggravating the flow of the nutrition. The nematode *G. strigosum* is a parasite commonly found in the stomach of Palearctic Lepordiae (Anderson 2000), such as rabbits and hares. Rabbits are most likely to be the original and best-adapted host, as they are able to tolerate the presence of *G. strigosum* much better than hares, where the nematodes cause serious stomach lesions. The pathology of rabbits, caused by infections with *G. strigosum*, is discussed (Cuquerella and Alunda 2009). An experimental infection of rabbits with *G. strigosum*, conducted by the authors, showed no alteration in hematological parameters (Cuquerella and Alunda 2009). They assumed that a higher burden of parasites may change the parameters. Specimens of the genus *Trichostrongylus* are small reddish nematodes, which are found in birds and ruminants (Anderson 2000). Several ruminant species are transmissible to rodents and lagomorphs, and zoonotic infections of some species have been reported in humans (Anderson 2000). *T. retortaeformis* is an abundant

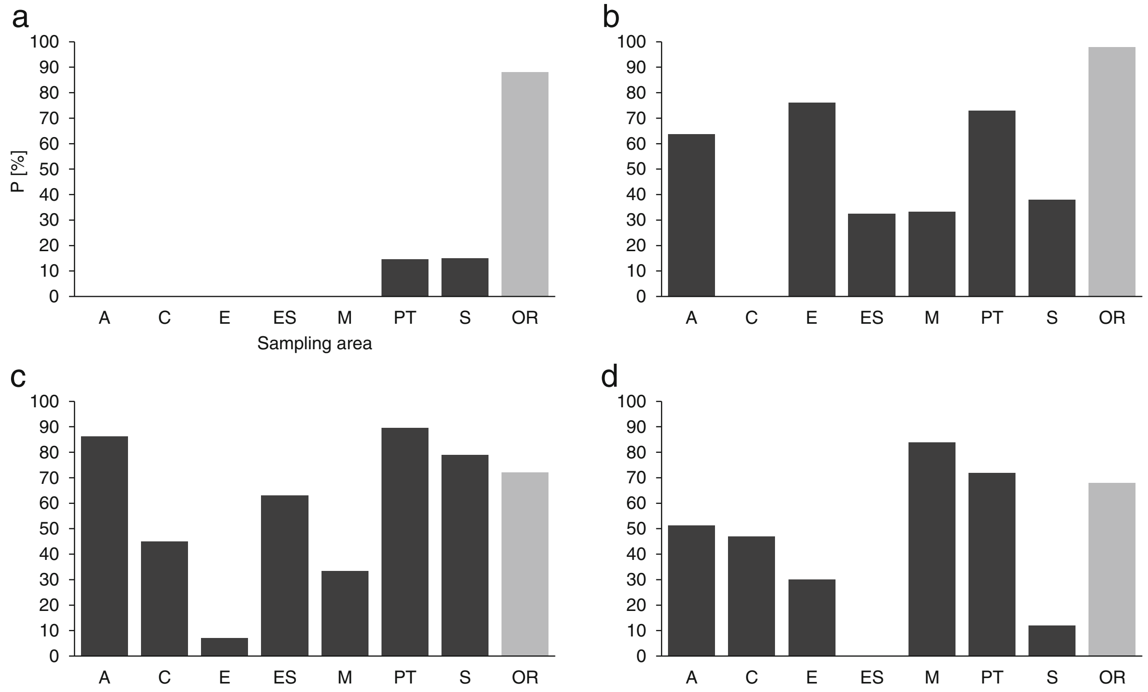


Fig. 11 Graphical illustration, comparison of prevalence (*P*) of four endoparasite species from international areas with own results (*OR*; *grey bar*). Prevalence of **a** *C. denticulata* and **b** *G. strigosum* constitutes a maximum, whereby rate of infections with **c** *T. retortaeformis* and **d** *P. ambiguus* reveals comparative high values. *A* Azores, *C* Canary Islands, *E* England, *ES* Spain, *M* Madeira, *PT* Portugal, *S* Scotland; *no bars shown* means no data recorded. Original source: Bull (1959), Boag (1988), Allan et al. (1999), Molina et al. (1999), Foronda et al. (2003a, b), and Eira et al. (2007)

parasite found in the small intestine of rabbits and hares (*Lepus europaeus*). *G. strigosum* and *T. retortaeformis* have a direct life cycle. Their free-living larval stages are sensitive to low temperatures and dry conditions (Cattadori et al. 2007). Infection occurs following the ingestion of the infectious third larval stage (L_3) (Anderson 2000). Cattadori et al. (2007) stated that the infection of both nematode species coincides with the rabbit reproductive period. According to these authors, these two species cause distinct infection patterns: the immune system of a young rabbit develops an immune response against *T. retortaeformis* during an ongoing infection. As a result, intensity of worm load increases, peaks, and decreases as the specimens age (Cattadori et al. 2007). In the case of *G. strigosum*, however, a convex age–intensity relationship cannot be observed and intensity rises with host age (Lello et al. 2004). In addition, cross-immunity of *T. retortaeformis* on *G. strigosum* infections is described by Lello et al. (2004). The third nematode species of interest, *P. ambiguus*, showed the highest value of intensity. Our results showed an intensity of 22,739 parasites in a single specimen, in addition to a consistently high abundance (1,247 parasites) and prevalence (68 %). Such infection rates are mainly based on the direct life cycle of the host. Eggs glue at the perianal skin and larvae develop inside until the infective third stage is reached (Boag et al. 2001). Then the infective larvae become ingested by grooming or via copraphagy (Boag et al. 2001). Although specimens were heavily infected by *P. ambiguus,* they were in general in a good condition due to the weak virulence of the nematode.

International situation

The comparison of our results (four endoparasitic helminths: *C. denticulata*, *G. strigosum*, *T. retortaeformis*, and *P. ambiguus*) with the results of preceding studies (Azores, Canary Islands (Tenerife), Madeira (Foronda et al. 2003a, b), England (Allan et al. 1999), Scotland (Boag 1988), New Zealand (Bull 1959), Portugal (Eira et al. 2007), and Spain (Molina et al. 1999)), made it possible to comment on the global dynamic nature of infection of these parasites found in *O. cuniculus*.

The prevalence of the cestode *C. denticulata* is higher (88 %) in the present study than the 15 % prevalence rate found in Scotland (Boag 1988) or the 14.7 % seen in Portugal (Eira et al. 2007) (Fig. 12a).

Possible reasons for the divergent values of prevalence in the area of investigation could be linked to the occurrence of oribatid mites. As mentioned above, the mites are required as intermediate hosts to complete the life cycle of *C. denticulata*. The spread of the tapeworm is therefore directly linked to its intermediate host. The high rates of infection likewise suggest high rates of infected oribatid mites on food plants in the

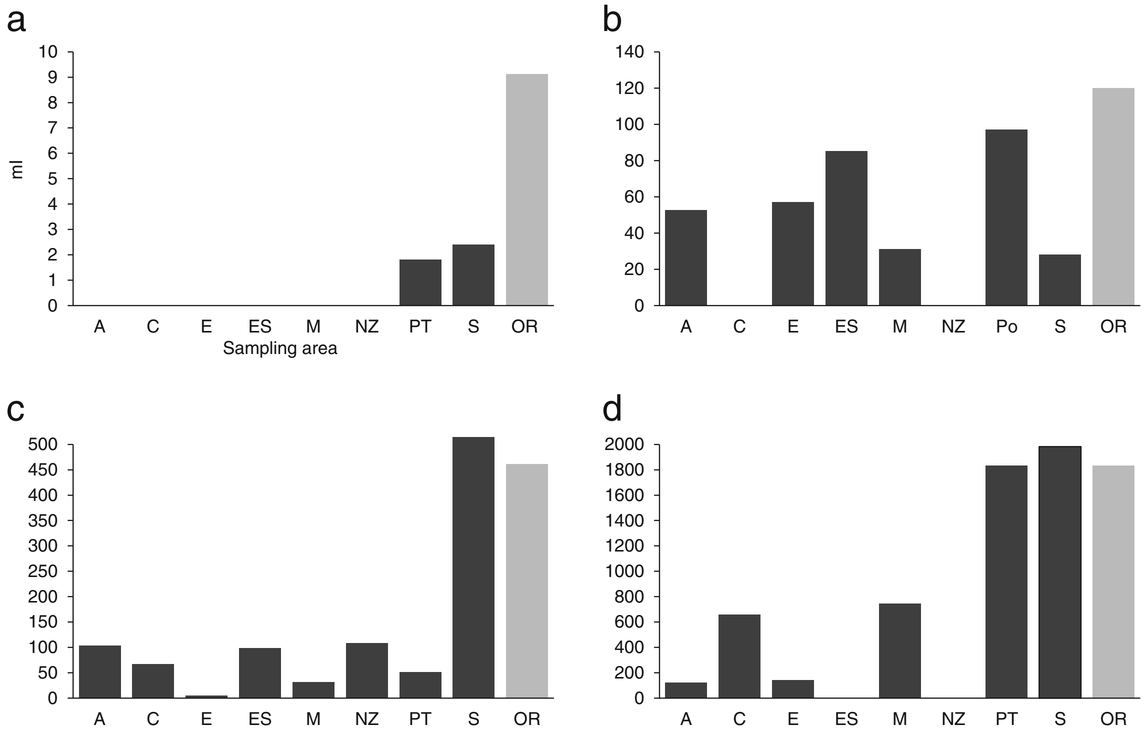


Fig. 12 Graphical illustration, comparison of mean intensity (*mI*) of four endoparasite species from international areas with own results (*OR*; *grey bar*). **a** *C. denticulata*. **b** *G. strigosum.* **c** *T. retortaeformis.* **d** *P. ambiguus*. Mean intensity varied with distinct numbers. Special amounts in mean intensity of *T. retortaeformis* and *P. ambiguus* differed enormously, partly over 10–fold. *A* Azores, *C* Canary Islands, *E* England, *ES* Spain, *M* Madeira, *NZ* New Zealand, *PT* Portugal, *S* Scotland; *no bars shown* means no data recorded. Original source: Bull (1959), Boag (1988), Allan et al. (1999), Molina et al. (1999), Foronda et al. (2003a, b), and Eira et al. (2007)

mentioned regions. Lower values of prevalence, as shown in the studies in Scotland (Boag 1988) and Portugal (Eira et al. 2007), may be explained by lower rates of infected intermediate hosts or their complete lack.

The prevalence (68 %) of *P. ambiguus* at the study site in Aachen is similar to the 71.8 % prevalence rate found in Portugal (Eira et al. 2007) but is lower than the 83 % prevalence found in Madeira (Foronda et al. 2003b) (Fig. 12). The lowest prevalence rate of *P. ambiguus* infecting rabbits was found in Scotland reaching 12 % (Boag 1988). The exorbitant intensity (22,739 *P. ambiguus* specimens found in a single rabbit in Aachen) can be explained by an over-dispersed distribution. Therefore, few host specimens of a population show extreme high or low values, respectively. Interestingly, Eira et al. (2007) reported an intensity of 1,833.5 *P. ambiguus*, which is similar to the mean value of intensity found in Aachen (Fig. 12). The present study identified a mean intensity (mI) of 1,834 *P. ambiguus* in the rabbit population. The mI from other studies showed significantly lower values. The high values of intensity reported by Foronda et al. (2003b), Boag (1988), and Eira et al. (2007) may be explained by the direct life cycle of this ageohelminth species, which facilitates its transmission (Foronda et al. 2003a). Factors affecting the intensity of *P. ambiguus* are seasonal shifts, acquired immunity (Foronda et al. 2003a), host weight (Allan et al. 1999), viral coinfections (Boag 1988), as well as sex and weight (Allan et al. 1999). Abiotic factors have less influence on intensity (Foronda et al. 2003a). However, bioclimatic factors have more impact on the occurrence of the geohelminth, *T. retortaeformis.* Foronda et al. (2003a) assumed that its presence is regulated by temperature and humidity. Further altering factors are sex and season, host resistance, and locality of collection (Bull 1959). Furthermore, availability of infective larvae is needed, which depends on host density and variations in climate and vegetation (Bull 1959). The comparison showed that infection with *T. retortaeformis* is heavily dependent on the factors mentioned above. Despite the collection of material during several periods in most studies, results are not homogeneous. In comparison, the values of prevalence (Fig. 11) show great variability reaching from 7 until 89.6 %. The values of mI (Fig. 12) for different areas of collection differ widely. Boag (1988) (mI=514) and own results (mI=461.36) reveal the highest values of mI. Further studies show significantly lower values (mI<103.3). Furthermore, values of mI and prevalence of the second geohelminth species *G. strigosum* vary among the compared studies (Figs. 11 and 12). Boag (1988) noted peaks of infection during summer and spring, these depend on natural factors. In addition, infection with myxomatosis also influences infection of rabbits with *G. strigosum*. As many authors gave no comments concerning viral infections, this biotic factor must be considered separately. Values of prevalence (Fig. 11) of rabbits from Azores, England, and Portugal are comparable to values obtained in Spain, Madeira, and Scotland. The prevalence rate noted at our collection site reached the highest value. Values of mI (Fig. 12) are grouped as follows: Madeira and Scotland showed lowest values, followed by Azores and England, while highest values were obtained in Spain and Portugal as well as in our own study. The distribution of this species is also linked to climatic factors: desiccation of infective L_3 stage larvae may limit the spread of *G. strigosum* (Allan et al. 1999). These authors also observed a positive correlation between effects of rainfall and an increasing worm burden, as well as a positive correlation between increasing host weights and the increasing burden of *G. strigosum*. According to Hernandez et al. (2013), the rabbit immune system may affect infection with *T. retortaeformis*. Interestingly, the biotic factor immune response does not or weakly affects *G. strigosum*, but is important in the case of *T. retortaeformis*. Parasitic helminths play a pivotal role in the ecosystem and in the food web structure and thus represent a considerable health and economic problem of global significance (Hernandez et al. 2013; Lafferty et al. 2006, 2008). During the last decades, evidence has shown that prevalence and intensity of helminths have increased in wildlife and livestock in temperate and subarctic regions, as a result of the rising temperature in these areas (Hernandez et al. 2013). The latter authors postulated analogous patterns, but obtained different rates of responses when *G. strigosum* and *T. retortaeformis* were exposed to similar climatic changes. Many helminths, especially nematodes, produce free-living larval stages. Their development and survival is strongly influenced by abiotic factors and stress tolerability (e.g., Anderson 2000; Klimpel and Rückert 2005). Experimental studies on soil-transmitted helminths have indicated that egg hatching and larval development were accelerated at higher temperatures (Saunders et al. 2002; van Dijk and Morgan 2008). This also provides an explanation for the high infection rates of humans in tropical countries. Eggs exposed to stochastic fluctuations in temperature develop faster when compared with constant or cyclic temperature regimes (Saunders et al. 2002). Recent studies have clearly identified the role of global warming in parasite dynamics (van Dijk and Morgan 2008; Studer et al. 2010; Paull and Johnson 2011). However, parasite response to climate change remains poorly understood. Cyclic simulations, based on two climatic decades, showed that more eggs hatched during the warmer decade than in the past colder period at a study site in Scotland (Hernandez et al. 2013). The authors postulated that the long-term climate warming might have induced a general positive effect on the hatching success of the nematodes *G. strigosum* and *T. retortaeformis*. Hernandez et al. (2013) also explain that the larval mortality increases proportionally with increasing temperature and discuss that the rabbits' immune system may has a different effect on each species. However, *T. retortaeformis* is much more influenced by the abiotic factor temperature than *G. strigosum*, and thus dies at a higher rate. These two nematode species have similar free-living stages and transmission strategies; they occur in similar habitats and commonly infect the same host. *T. retortaeformis* survived much better than *G. strigosum* under similar climatic conditions (Hernandez et al. 2013).

According to Audebert and Durette-Desset (2007), the advantage of selection may be explained by phylogenetic differences between *G. strigosum* and *T. retortaeformis*. Hernandez et al. (2013) considered direct and indirect influences of contrasting interactions with the host on hatching success. The host immune response could change the quality of eggs shed in rabbit feces, or the parasite immune processes could affect the physiology of female worms.

Hernandez et al. (2013) showed that egg hatching and larval survival reached highest values in summer, compared with colder spring and autumn. They confirmed reports of higher risk of infections with soil-transmitted helminths in animal populations during spring–summer month (Pandey 1974; May and Anderson 1979; Smith et al. 1987; Anderson 2000; Cattadori et al. 2005; Cornell et al. 2008; Hernandez et al. 2013). In accordance with previous studies on other helminthic species, the authors confirmed that parasite hatching is low to negligible in these temperate areas during the cold months (Crofton 1948; Prasad 1959; Gupta 1961; Rogers and Sommerville 1963; Stromberg 1997). In conclusion, the investigated rabbit specimens from the surroundings of Aachen showed remarkable similarities in the composition of their endoparasite fauna compared with other studies. They are in clear accordance with the results obtained in other geographical regions, especially in Europe. Wild rabbits were introduced into several new ecosystems, causing severe ecological consequences, e.g., in Australia and Mauritius (North et al. 1994; White and Newton-Cross 2000). The ability of rabbits to adapt is limited by ecological differences in the native habitats, such as temperature and composition of flora. The observed climate change in the past 60 years did not inhibit the worldwide spread of wild rabbits, so that the area colonized by rabbits amounts to approximately 11 million km^2 today (IPCC 2007; Flux and Fullagar 2008). The mentioned ability, to adapt to new regions, is probably the strongest factor permitting further spread. The changes in landscape, from forested areas to open areas used for agricultural use or for building of human dwellings, are favorable for rabbits. Thereby the possibility to disperse zoonotic pathogens close to human-inhabited areas is growing. The rising consumption of rabbit meat obtained from breeding farms or from hunted wild rabbits is a further reason to investigate rabbit parasites as it is expected that parasites may cause economic losses to breeding farms. The amount of produced rabbit meat has risen significantly since the early records in 1964 by the FAO. The worldwide highest rates of consumption were 1,867,788 t in 2007 and 1,712,557 t in 2011 (FAO 2013). In addition to economic aspects, health implications connected to rabbit meat consumption must be considered.

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