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ORIGINAL PAPER

Parasites of two abundant sympatric rodent species in relation to host phylogeny and ecology

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Abstract In the present study, two abundant sympatric rodent species (27 *Apodemus flavicollis* and 33 *A. sylvaticus*) were studied for their endo- and ectoparasite fauna. The rodents were trapped in Dormagen, a city in North Rhine–Westphalia, Germany. A total of 20 different parasites species were identified, 13 endoparasite (2 Digenea, 5 Cestoda and 7 Nematoda) and 7 ectoparasite (5 Insecta and 2 Arachnida) species. Thirteen parasite species were found inhabiting both rodent species. The predominant endoparasite species in both rodents was the nematode *Pelodera strongyloides*, followed by the nematode *Heligmosomoides polygyrus* and a *Syphacia* species. The flea *Ctenophthalmus agyrtes* was the dominant ectoparasite in both rodent species. *A. flavicollis* usually carried 1–7 ecto-/endoparasite species (mean 4.0), whereas *A. sylvaticus* were mostly infested with 1–9 (mean 4.4). The parasite diversity of *A. flavicollis* (H'=0.268, J=0.097) was marginal lower in comparison to *A. sylvaticus* (H'=0.319, J=0.110). The two rodent species examined show remarkable similarities in the composition of their endo- and ectoparasite fauna being directly related to their similar pattern of living in the investigated area.

Introduction

Parasites are a driving force in the process of evolution. Parallel to the abiotic environment, and, among other biotic factors, they generate a pressure for selection and adaptation to their hosts, which can result in elimination of genes or in new combination of genes in the host genome (Benz 1995).

Parasites differ markedly in their degree of host specificity, and the extent to which relationships between hosts are reflected (Holmes and Price 1980). The host phylogeny and evolutionary adaptation between host and parasite constitute the recruitment and establishment of a parasite in its host (Lile 1998). Other biotic and abiotic factors such as feeding ecology, habitat preferences, host age and sex, host physiology and climatic conditions may also influence the relationship between parasite and host (e.g. Behnke et al. 2001; Klimpel et al. 2003, 2006; Krasnov et al. 2005). Consequently, related host species with similarities in their habitat and diet may result in similar or even identical parasite faunas (Muñoz et al. 2006).

Therefore, parasites can be divided into specialists and generalists related to their host preferences and specificity (Holmes and Price 1980). For specialists, the evolution of host and parasites has been parallel, and phylogenetically related hosts can therefore harbour the same specialist parasite species, whereas generalists have the ability to expand the number of host species suitable for completing their lifecycles (Lile 1998).

Furthermore, parasites are an essential part of every ecosystem, representing a major factor in global biodiversity. Their presence becomes evident after a massive propagation, causing diseases and sometimes even leading to mass mortality of infested intermediate, reservoir or final hosts. Rodents have a greater ability than most other animal species to harbour many zoonotic agents, and in combination with their broad distribution and their neighbourhood of domestic animals and humans, they play an important role as reservoir host for vector-borne diseases agents (e.g.

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Salmonella spp., hantaviruses, *Babesia* spp., *Echinococcus* spp.). Recently, 24 known human-pathogenic vector-born diseases agents are transmitted, from these 13 by hard ticks, 3 by mosquitoes, 1 by body lice and 5 by rodents (Faulde and Hoffmann 2001).

The rodent family Muridae is the largest mammalian family and contains 1,326 species, which are divided into 17 subfamilies (Martin et al. 2000). In Europe, five genera of the subfamily Murinae (mice and rats) are present. Field mice, of the genus *Apodemus*, are the most common rodents and inhabit broadleaf forests in the temperate zone of Palearctic region (Serizawa et al. 2000; Reutter et al. 2003). Members of *Apodemus* show a species-specific limited distribution, often in coexistence with two sympatric species (Reutter et al. 2003). Until now, approximately 20 different species of *Apodemus* are recognized world wide; half of them have a geographic distribution in Asia and half of them in Europe, whereas a few having a global distribution (Serizawa et al. 2000). The both abundant species in the northern part of Europe are the yellow-necked mouse *Apodemus flavicollis* and the wood mouse *A. sylvaticus*.

The helminth parasite fauna of wild rodents in Europe, especially of *A. flavicollis* and *A. sylvaticus*, has been well-documented and is known to be affected by abiotic and biotic factors (e.g. Lewis 1987; Behnke et al. 1999, 2001; Ferrari et al. 2003). So far, an in depth investigation concerning the metazoan ecto- and endoparasite fauna of both *Apodemus* species inhabiting the same area has not been performed. The aim of the present study was to firstly explore the metazoan parasite fauna of two abundant sympatric rodent species in the same area and to investigate the roles of host phylogeny and ecology in the formation of their parasite fauna.

Materials and methods

Sample collection

The rodents analysed in this study were captured using commercial quality metal live double traps as a part of studies investigating hantavirus infections of small wildlife animals. Rodents were trapped at Dormagen (51°05′40″N, 006°50′30″E), a small town near the city of Düsseldorf in North Rhine–Westphalia, Germany. The trapping sites were selected on the basis of reported human cases of suspected hantavirus infections, where exposure to rodents was considered to be likely. A total of 40 double traps was set in the early evening and was collected at the beginning of the next day. Trapping was carried out over an 81-days period from the 10th of May to the 22nd of September 2005.

Parasitological examination

After trapping, the rodents were transported separately to the laboratory at the University of Düsseldorf and were euthanized by exposure to a CO_2-saturated atmosphere in a glass covered with a cap. Before examination, each rodent specimen was measured for morphometric data such as head–body length (HBL) and total weight (TW), which were recorded to the nearest 0.01 cm and 0.01 g. The ears, coat, skin, nostrils and after of each rodent specimen were firstly studied for ectoparasites. Then, the body cavity was opened, and the alimentary tract was removed for further examinations. The body weight (BW, to the nearest 0.1 g) of each disembowelled rodent was recorded. All organs were separated from the surrounding fat tissue and placed in Petri dishes containing physiological saline solution and were examined for endoparasites under a dissection microscope.

Isolated parasites were fixed in 4% borax-buffered formalin and preserved in 70% ethanol/5% glycerine. For identification purposes, nematodes were dehydrated in a gradated ethanol series and transferred to 100% glycerine (Riemann 1988). Digenea and Cestoda were stained with acetic carmine, dehydrated, cleared with eugenol or creosote and mounted in Canada balsam. For species determination, all ectoparasites were cleared in 10% KOH, dehydrated and mounted in Canada balsam. Parasite identification literature included original descriptions.

Data analyses

The parasitological terminology used follows Bush et al. (1997): prevalence (P) is the number of infected rodents with one or more individuals of a particular parasite species (or taxonomic group) divided by the number of hosts examined (expressed as a percentage); intensity (of infection; I) is the number of individuals of a particular parasite species in a single infected host (expressed as a numerical range); mean intensity (of infection; mI) is the average intensity, that means, it is the total number of parasites of a particular species found in a sample divided by the number of infected hosts; and abundance (A) is the total number of individuals of a particular parasite species in a sample of a particular host species divided by the total number of hosts of that species examined, including both infected and uninfected hosts.

The diversity of the metazoan parasite fauna of each rodent species was estimated by using the Shannon–Wiener diversity index (H') and the evenness index (J) of Pielou (Magurran 1988).

Multivariate statistical analyses were performed to examine differences in the parasite fauna of two different *Apodemus* species. Only rodents with more than nine parasite specimens were included in this analysis. Before

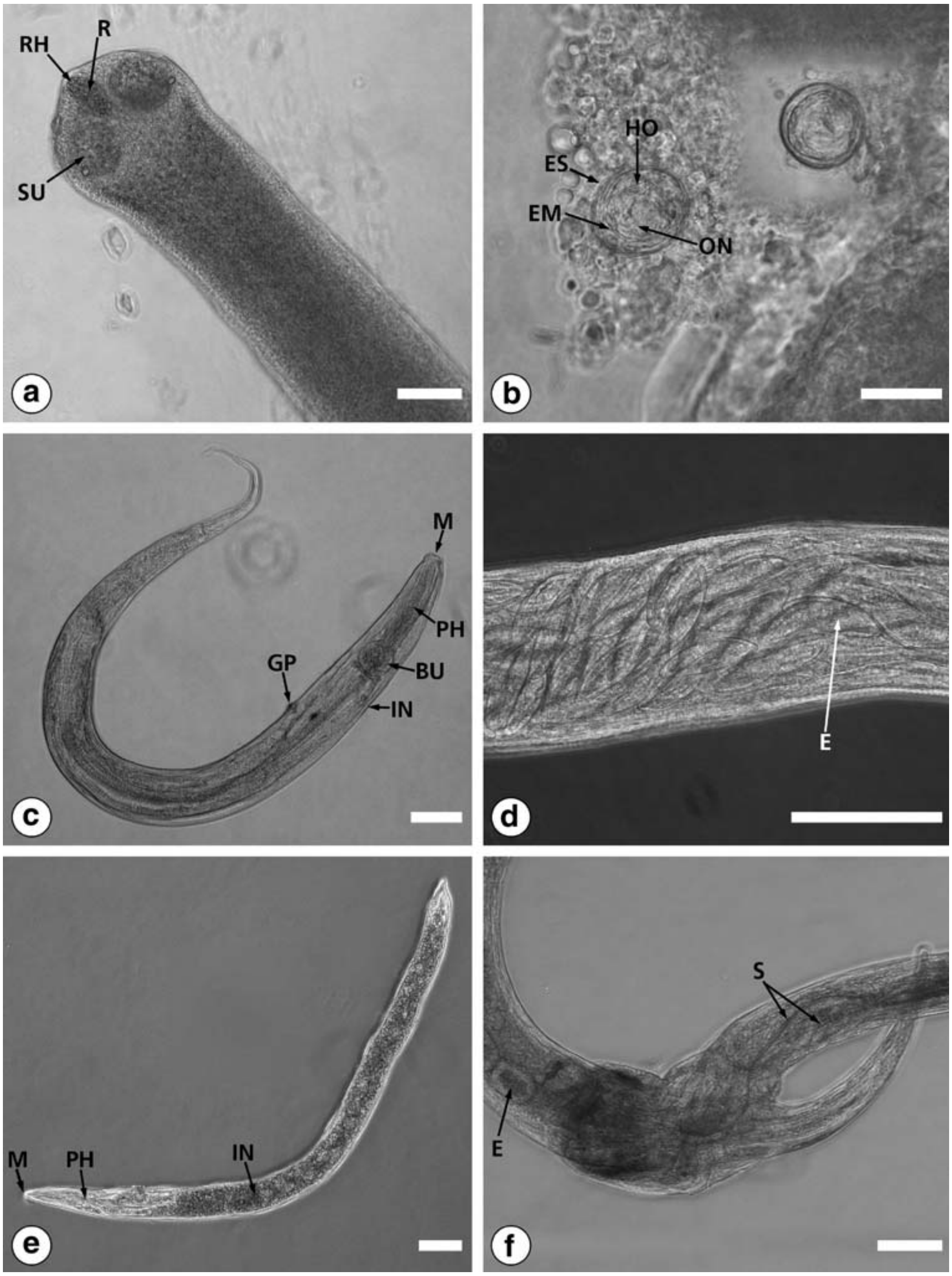


Fig. 1 Light micrographs of different endoparasites isolated from *Apodemus flavicollis* and *A. sylvaticus*. **a** Scolex of *Microsomacanthus murissylvatici* (scale bar 0.18 mm) and **b** eggs within oncosphaera (0.018 mm); **c** habitus of a young and fertilized female of *Syphacia* cf. *obvelata* (0.29 mm) and **d** a uterus filled with eggs (0.21 mm); **e** third larva of *Pelodera strongyloides* (0.07 mm); **f** copulation of a male and female of *Heligmosomoides polygyrus* (0.15 mm). *BU* bulbus, *E* egg, *EM* embryophore, *ES* egg shell, *GP* genital pore, *HO* hooks of oncosphaera, *IN* intestine, *M* mouth, *ON* oncosphaera, *PH* pharynx, *R* rostellum, *RH* rostellar hooks, *S* spiculae, *SU* sucker

analysis, the data were fourth-root transformed. The transformation reduced the weighting of dominant species and increased the importance of rare ones (Field et al. 1982). The similarity between rodent specimens was calculated by means of the Bray–Curtis measure (Bray and Curtis 1957; Field et al. 1982). Samples were classified by hierarchical agglomerative cluster analysis using the group-average linking method and ordinated using non-metric, multi-dimensional scaling techniques (MDS, Kruskal 1964; Kruskal and Wish 1978). All multivariate analyses were carried out using subroutines of the Primer-E (Version 5.2.2).

Results

In the present study, for the first time, the endo- and ectoparasite fauna of 27 *A. flavicollis* (HBL 7.24–10.32 g, mean 8.91 cm; TW 16.33–39.42 g, mean 27.46 g) and 33 *A. sylvaticus* (HBL 6.02–9.71 cm, mean 8.16 cm; TW 9.89–30.30, mean 21.76 g) from the same investigation area at the town of Dormagen (northwestern Germany) were analysed. A total of 20 different parasite species were identified, 13 endoparasite and 7 ectoparasite species (Figs. 1, 2). Thirteen parasite species were found inhabiting both rodent species. The site of infestation, prevalence, intensity, mean intensity

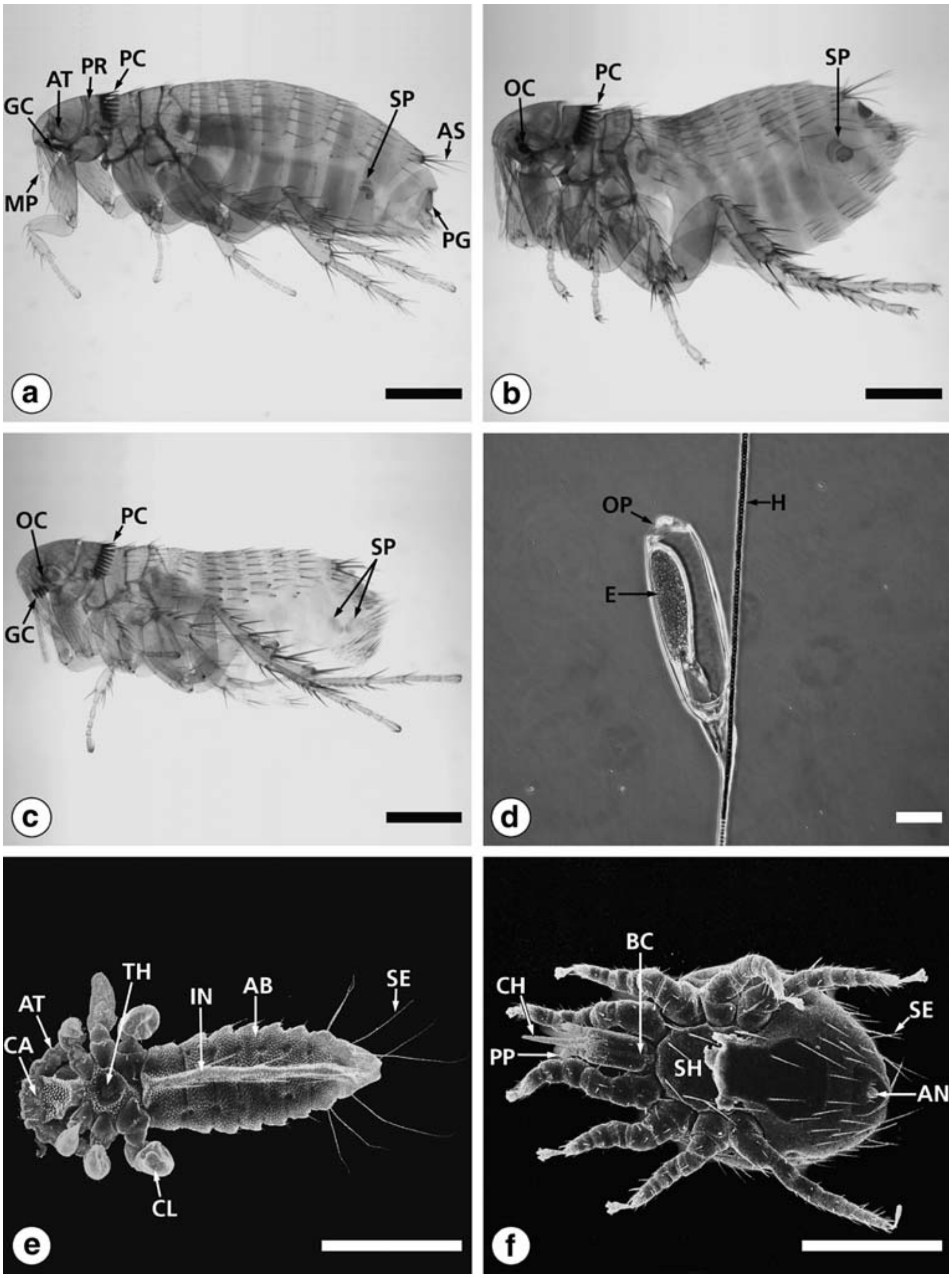


Fig. 2 Light and scanning electron micrographs of different ectoparasites isolated from *Apodemus flavicollis* and *A. sylvaticus*. **a** Female of *Ctenophthalmus agyrtes* (scale bar 0.57 mm); **b** female of *Nosopsyllus fasciatus* (0.57 mm); **c** female of *Typhloceras poppei* (0.65 mm). **d** Egg of *Polyplax serrata* on a hair of *A. sylvaticus* (0.11 mm); **e** habitus of *P. serrata* (0.21 mm) and of **f** *Laelaps agilis* (0.78 mm) from the coat of *A. sylvaticus*. *AS* antensilial seta, *AB* abdomen, *AN* anus, *AT* antenna, *BC* basis capituli, *CA* caput, *CH* chelicera, *CL* claw, *E* egg, *GC* ctenidium (genal comb), *H* rodent hair, *IN* intestine, *MP* maxillary palp, *OC* ocellus, *OP* operculum, *PC* pronotal comb (ctenidium), *PG* pygidium, *PP* pedipalps, *PR* pronotum, *SE* seta, *SH* sternal shields, *SP* spermatheca, *TH* thorax

and abundance for each parasite and rodent species are given in Table 1.

Parasite composition

Apodemus flavicollis

In total, 16 different parasite species were found: one Digenea species, four Cestoda species, five Nematoda species, four Insecta species and two Arachnida species. The predominant parasite species was the nematode *Pelodera strongyloides*, followed by the nematodes *Heligmosomoides polygyrus* and *Syphacia* cf. *obvelata*. Three parasite species (*Dilepis undula*, *Microsomacanthus murissylvatici*, *Taenia pisiformis*) were found only in *A. flavicollis* (Table 1).

Apodemus sylvaticus

A total of 17 parasite species were identified belonging to the groups Digenea (two species), Cestoda (one species), Nematoda (seven species), Insecta (five species) and

Table 1 Prevalence (P), mean intensity (mI), intensity (I) and abundance (A) of infestation of both *Apodemus* species

		Rodent species					
		A. flavicollis			*A. sylvaticus*		
Parasite species	adult/larva	P (%)	mI (I)	A	P (%)	mI (I)	A
Digenea							
B. recurva	a				6.0	1.5 (1–2)	0.09
C. vitta	a	33.3	12.4 (1–38)	4.15	21.2	7.9 (1–24)	1.67
Cestoda							
D. undula	a	3.7	1.0 (1)	0.04			
M. murissylvatici	a	3.7	9.0 (9)	0.33			
P. matovi	a	11.1	3.3 (1–8)	0.37	33.3	6.0 (1–17)	2.00
T. pisiformis	l	3.7	1.0 (1)	0.04			
Cestoda indet.	l				3.0	2.0 (2)	0.06
Nematoda							
A. murissylvatici	a	18.5	5.6 (1–17)	1.04	33.3	12.3 (1–78)	4.09
E. gastricus	a				18.2	6.0 (1–17)	1.09
H. polygyrus	a	85.2	23.9 (1–89)	20.41	78.8	24.7 (1–109)	19.42
H. spumosa	a				3.0	1.0 (1)	0.03
P. strongyloides	a	51.9	402.9 (4–2324)	208.93	72.7	289.9 (2–2120)	210.88
Syphacia cf. *obvelata*	a	37.0	39.4 (1–156)	14.59	30.3	18.6 (1–113)	5.64
Syphacia cf. *stroma*	a	3.7	12.0 (12)	0.44	27.3	107.1 (6–646)	29.21
Insecta							
C. agyrtes	a	59.3	2.1 (1–6)	1.26	54.6	2.1 (1–6)	1.12
H. acanthopus	a				3.0	3.0 (3)	0.09
N. fasciatus	a	22.2	1.3 (1–3)	0.30	15.2	1.0 (1)	0.15
P. serrata	a	3.7	1.0 (1)	0.04	3.0	2.0 (2)	0.06
T. poppei	a	3.7	2.0 (2)	0.07	6.0	2.0 (1–3)	0.46
Arachnida							
I. ricinus	l	14.8	9.0 (4–17)	1.33	24.2	3.3 (1–15)	0.79
L. agilis	a	48.2	2.7 (1–7)	1.30	12.1	1.8 (1–4)	0.21

Arachnida (two species). *P. strongyloides* was the predominant parasite species followed by the both nematode species *Syphacia* cf. *stroma* and *H. polygyrus*. Four parasite species (*Brachylaima recurva*, *Eucoleus gastricus*, *Heterakis spumosa*, *Hoplopleura acanthopus*) were only isolated from *A. sylvaticus* (Table 1).

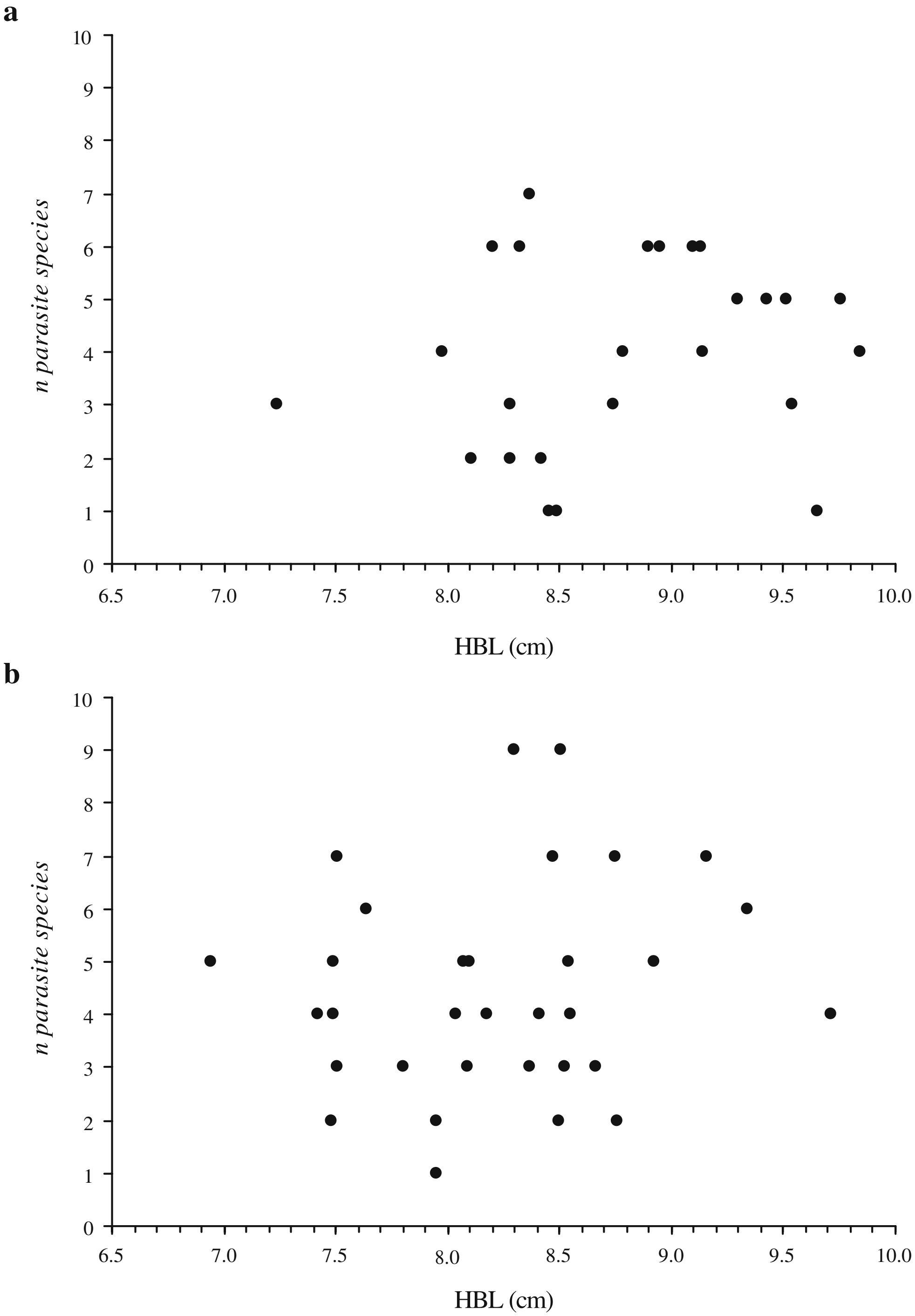
Parasite diversity and species assemblages

The parasite fauna of both *Apodemus* species is highly diverse and similar. *A. flavicollis* usually carried 1–7 ecto-/endoparasite species (mean 4.0), whereas *A. sylvaticus* were mostly infested with 1–9 (mean 4.4). Separated in ecto- and endoparasites, *A. flavicollis* possessed 1–5 (mean 2.5) endoparasite species, and *A. sylvaticus* harboured 1–6 (mean 3.2) species. The number of ectoparasite species in both rodents ranged from 0–4 (mean 1.5) and 0–3 (mean 1.2), respectively (Fig. 3a,b and Fig. 4). The parasite diversity of *A. flavicollis* (H'=0.268, J=0.097) was marginal lower in comparison to *A. sylvaticus* (H'=0.319, J=0.110). The cluster analyses and the associated MDS plot for specimens investigated either of *A. flavicollis* or *A. sylvaticus* showed no significant arrangement in groups concerning the infestation with ecto-/endoparasites. Therefore, no differences exist for the infestation with parasites for both the *Apodemus* species investigated (Fig. 5a,b).

Discussion

The present study gives a first detailed overview about the parasite fauna of two abundant field mouse species (*A. flavicollis*, *A. sylvaticus*) from the same ecological habitat. *A. sylvaticus* is distributed in almost every parts of Europe including Germany. The parasite fauna of *A. sylvaticus*, especially the helminths, has been the focus of numerous investigations in different parts of Europe (e.g. Behnke et al. 1999; Fuentes et al. 2004). Among various rodent species investigated, *A. sylvaticus* harbours the greatest number of different parasite species (e.g. Feliu et al. 1997). *A. flavicollis* can be regarded as a sister-species of *A. sylvaticus* and shares a similar distribution.

Fig. 3 Number of different parasite species in comparison to the HBL, **a** *Apodemus flavicollis* and **b** *A. sylvaticus*



In contrast to *A. sylvaticus*, the parasite fauna of *A. flavicollis* has only scarcely been investigated (e.g. Lewis 1987). However, the parasite fauna of *A. flavicollis* seems to be identical to that of *A. sylvaticus*.

Corrigia vitta was the most abundant species from the two digenean species isolated. *C. vitta* is a typical digenean of both *Apodemus* species. The lifecycle is unknown, but it is assumed to parallel the life histories of other dicrocoeliid digeneans (Lewis 1968). The genus *Brachylaima* (Brachylaimidae) includes trematodes of birds and mammals as final hosts, with land snails and slugs as their first and second intermediate hosts (Dawes 1968). The infection of *A. sylvaticus* with *B. recurva* occurs by feeding of snails, but regarding the low infestation rate of *A. sylvaticus*, the snails must have been only a minor component of the rodent diet within the time space shortly before trapping.

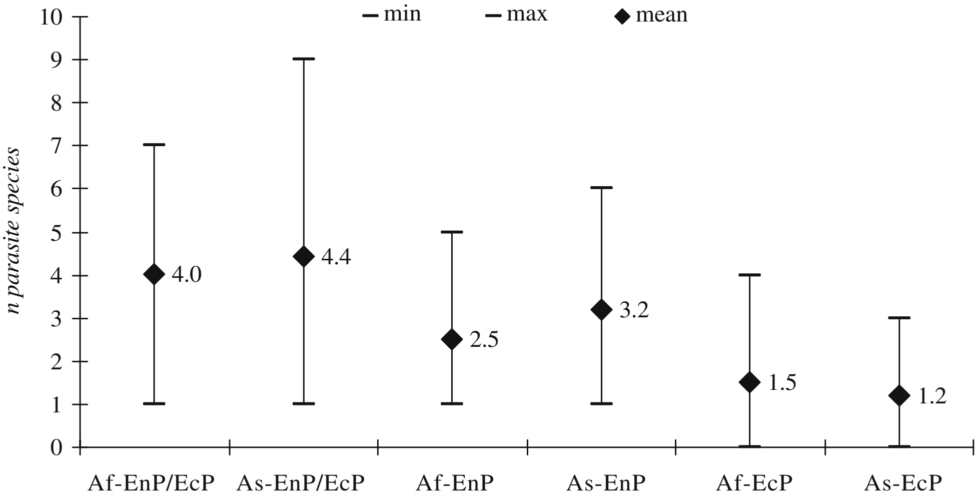


Fig. 4 Number of parasite species (*n*) in mean, minimum and maximum value of endo- and/or ectoparasites in *Apodemus flavicollis* (*Af*) and *A. sylvaticus* (*As*). *EcP* ectoparasites, *EnP* endoparasites

Four parasite species belonging to the Cestoda were detected. *D. undula* is a typical parasite of passerine birds (e.g. thrushes) and occurs accidentally in *A. flavicollis* (Świderski et al. 2004). *M. murissylvatici* was only isolated from the intestine of *A. flavicollis*. *M. murissylvatici* is also found among other Muridae as well as Arvicolidae. Its lifecycle is unknown, but it is assumed that fleas of the genus *Ctenophthalmus* act as intermediate hosts (Lewis 1987). *C. agyrtes* were found in high numbers on both mouse species examined. This fact affirms the thesis of Lewis (1987) mentioned above. Hitherto, the cestode species *Pseudocatenotaenia matovi* has been found only in *A. flavicollis* and *A. sylvaticus*. The lifecycle of *P. matovi* is unknown, but it seems to be a specific parasite for both of these rodent species. One liver cyst (cysticercus) of *T. pisiformis* was found in one *A. flavicollis*. The normal intermediate hosts for this cestode are Leporidae (e.g. hares, rabbits), whereas free-living or domesticated carnivores (especially foxes, dogs and cats) are the definitive hosts for *T. pisiformis* (Cheng 1986; Lucius et al. 1988).

The most abundant species in both rodents were the nematodes *P. strongyloides*, *H. polygyrus* and the species of the genus *Syphacia*, as in the majority of previous studies in other European localities. Oxyuroid nematodes or pinworms are common intestinal parasites of both wild and laboratory rodents (Lewis 1987). Especially, nematodes of the genus *Syphacia* can accumulate to a high abundance through autoinfection, facilitated by eggs that are infective within hours of being released by female worms onto the perianal surface of the host (Lewis 1968; Behnke et al. 2001).

P. strongyloides is a small free-living saprophytic nematode species that normally completes its entire lifecycle in organic matter (Saari and Nikander 2006). The third-stage larvae are capable of invading the skin of rodents, and, in a few cases only, they cause a dermatitis in several mammalian species (e.g. dogs; Hominick and Aston 1981; Saari and Nikander 2006). *H. polygyrus* is a trichostrongylid nematode found in small rodents. Its lifecycle is direct and involves both free-living and parasitic stages (Anderson 2000). The prevalence of *H. polygyrus* is frequently high in populations of *A. flavicollis* and *A. sylvaticus* and correspondents to results obtained in the British Isles (Lewis 1987). The nematode *Aonchotheca murissylvatici* is a common parasite in the digestive tract of different rodent species. Infection takes place by the ingestion of eggs-contaminated diet. The statement of Ashour et al. (1994) that *A. murissylvatici* acts as a zoonotic parasite causing capillariasis in humans has not been confirmed. Since 35 years, it is known that *E. gastricus* is an intestinal parasite of *A. sylvaticus* (Memaran 1970). The lifecycle of *E. gastricus* is not described, but it is assumed that earthworms (e.g. *Lumbricus terrestris*) serve as intermediate and reservoir hosts (Skrjabin et al. 1957).

The Heterakidae (nematode) are intestinal parasites of numerous avian and mammalian species. The adult nematodes live in the caeca of their hosts. *H. spumosa* is one species of the family Heterakidae and a most common parasite in mice and rats and is sometimes found in hedgehogs. The infection occurs by oral uptake of embryonated eggs.

The fleas, e.g. *Ctenophthalmus agyrtes* are prevalent ectoparasites of wild mammals and especially of rodents. Fleas can act as vectors for zoonotic pathogens for mammals and also for humans (Lewis 1993). The European rat flea (*Nosopsyllus fasciatus*) is found worldwide as an ectoparasite of *Rattus* spp., other rodents, sometimes on domestic animals and rarely on humans (Visser et al. 2001). The species is well known as vector for numerous pathogens (e.g. *Yersinia pestis*, *Salmonella* spp., *Hymenolepis* spp.). *Typhloceras poppei* is often found on rodent nests but unusually as ectoparasite on rodents (Peus 1972) and only scarcely on cats (Visser et al. 2001).

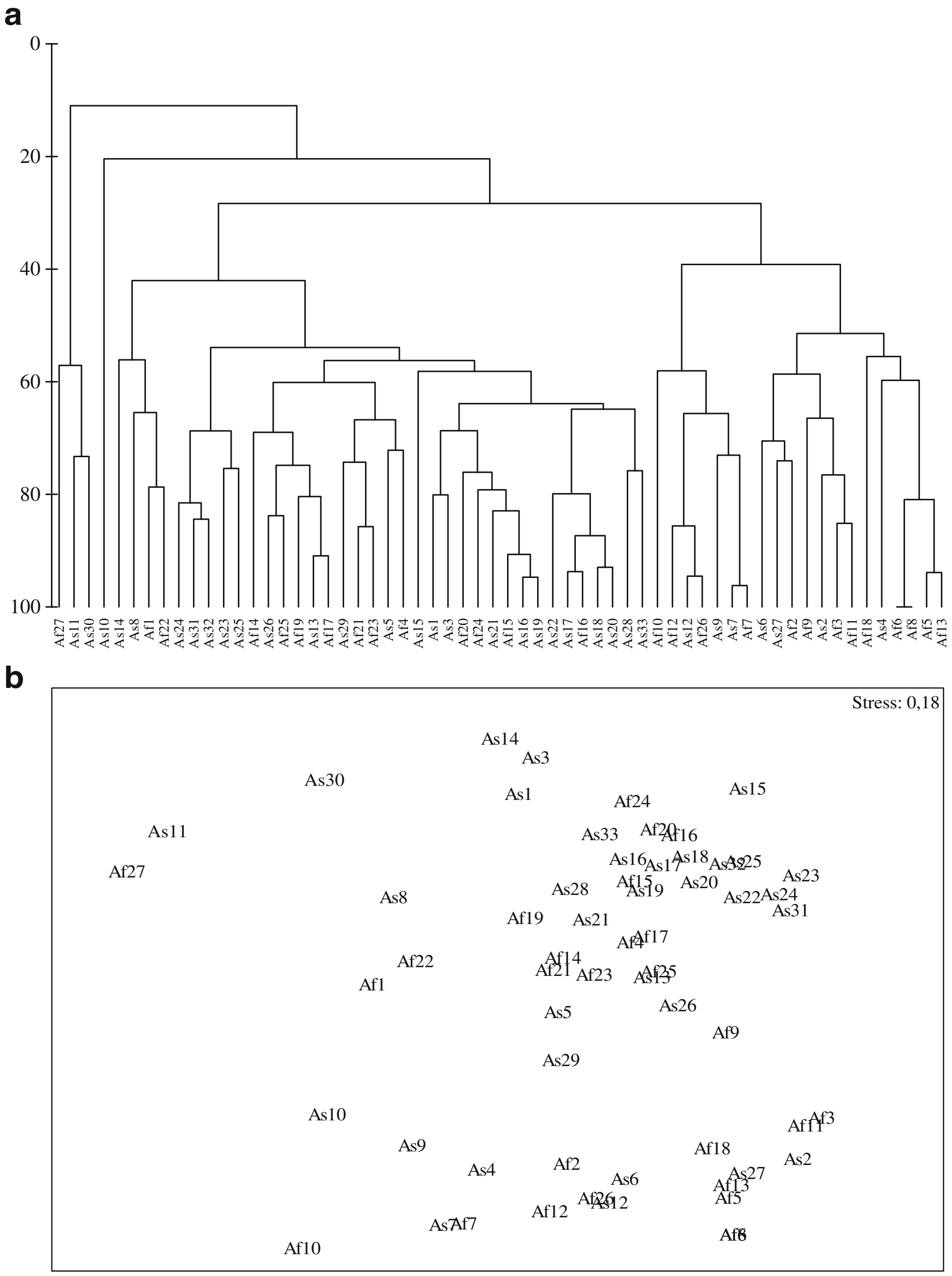


Fig. 5 Classification of parasites assemblages in the two investigated *Apodemus* species. Cluster analyses **a** and corresponding MDS plot **b**. Labels indicate the *Apodemus* species and number (*A. flavicollis*, Af 1–27; *A. sylvaticus*, As 1–33)

Both Anoplura species *Polyplax serrata* and *H. acanthopus* are common parasites of rodents.

The hard tick *Ixodes ricinus* is a vector of important pathogens, for example, different *Borrelia* spp., viruses, *Babesia* spp., and is to be found on mammals, birds and also reptiles. In both investigated *Apodemus* species, the larvae of *I. ricinus* were frequently encountered, whereas the nymphae were scarce. The family Laelapidae includes a large number of different genera; its taxonomy is difficult because of the lack of careful descriptions. *Laelaps agilis* is a permanent heteroxenous ectoparasite and frequently found on earth dwelling small mammals and in their nests (Karg 1994).

In conclusion, the two rodent species investigated show remarkable similarities in the composition of their endo- and ectoparasite fauna being directly related to their similar pattern of live. The results demonstrate that phylogenetically related host species can harbour a similar parasite fauna. Furthermore, *A. flavicollis* and *A. sylvaticus* possess high similarities between their metazoan parasite faunas because they have similar dietary and environmental requirements.

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