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Intestinal helminth communities of *Sorex* shrews in Finland

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The fauna and infection levels of intestinal helminths in three species of *Sorex* shrews (*S. araneus*, *S. caecutiens* and *S. minutus*) were studied in various parts of Finland. Altogether 23 species of helminths were recovered, representing trematodes (4 species), cestodes (14 species) and nematodes (5 species). The total number of helminth species, the helminth burden and the number of species per host were all higher in *S. araneus* than in the other shrew species. This pattern was evident both in local populations and in combined material from Finland, and has been observed for shrew communities in other geographical regions. The present analysis suggests that *S. araneus* harbours heavy helminth burdens because of its large size, wide diet and great abundance.

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1. Introduction

Sorex shrews are characterized by relatively diverse and abundant communities of intestinal helminths, especially cestodes and trematodes, which may be related to the opportunistic feeding habits of shrews (Dogiel 1964). Kennedy et al. (1986) have shown that diverse helminth communities are typical of birds and fish hosts with broad diets, whereas selective feeding on potential intermediate hosts of helminths often leads to abundant but less diverse helminth communities (see also Stock & Holmes 1987).

In northern Europe five species of shrew in the genus *Sorex* occur sympatrically. These species comprise a practically non-overlapping series in size and exhibit differences in other aspects of their biology, including physiology, abundance, habitat and food selection (Hanski 1990). Although the helminths of *Sorex* shrews that have been studied so far are not strictly host specific (Soltys 1954, Prokopic 1958, Vaucher 1971), the various host species seem to differ as resources for helminths. In addition to diet, two other characteristics of shrews may affect the diversity and abundance of their helminth communities. First, the size of the host species may be important in determining the density and species richness of parasites in individual hosts. The absolute amount of food consumed, which is related to body size, affects the colonization rate of infective stages. Furthermore, the length and the volume of the intestine may affect the equilibrium density of intestinal helminths. Secondly, the size or the density of the host population may affect the transmission efficiency of helminths, thereby affecting the helminth diversity and abundance.

The purpose of this study is to characterize the fauna and community structure of intestinal helminths in three species of *Sorex* shrews, *S. araneus*, *S. caecutiens* and *S. minutus*, in Finland. Specifically, I attempt to relate the differences between the shrew species in the occurrence and abundance of helminths to their diet, size and population density. Interspecific patterns are investigated at two spatial levels, at the level of local populations and in pooled samples for the whole of Finland. Additionally, the helminth communities of shrews in Finland are compared with those in other geographical regions (British Isles, Central Europe, USSR) and with helminth communities in other host species.

2. Material and methods

A total of 109 shrews belonging to the species *Sorex araneus* (*n*=69), *Sorex caecutiens* (*n*=30) and *Sorex minutus* (*n*=10) was studied for intestinal helminths. The shrews were trapped in several localities in southern and northern Finland in 1985–1988.

A proportion of the material (*n*=26), including both young (immature) and old (overwintered, mature) shrews, was studied for faunistical purposes only, while the remaining 83 shrews, all of which were young immature individuals caught in August–September, were studied quantitatively. Most of the latter individuals were trapped in three areas: Lapland (localities Pallasjärvi and Kilpisjärvi), eastern Finland (Kainuu: localities Paljakka, Kajaani, Sotkamo) and southern Finland (Hanko), in 1987 and 1988. *Sorex araneus* and *S. minutus* were represented in all three samples, while *S. caecutiens* was collected only from Lapland and eastern Finland. Two of the eight individuals of *S. minutus* examined quantitatively were obtained from outside the main study areas.

In Lapland and eastern Finland the shrews were caught from spruce (*Picea abies*) and pine (*Pinus vulgaris*) forests with a thick moss layer. In the southern locality trapping was conducted in patches of moist deciduous forest dominated by alder (*Alnus glutinosa*). Shrews were trapped using snap-traps, pitfalls and live-traps. They were dissected immediately after being caught or frozen for later examination. The stomach and intestine were examined microscopically for helminths (the smallest tapeworms in shrews hardly reach 1 mm in length). The specimens that could not be identified under the binocular microscope were studied at a higher magnification using aqueous preparations. A series of permanently mounted specimens were used for comparison.

The specific identification of helminths is based on the monographs of Zarnowski (1960), Vaucher (1971), Vaucher & Durette-Desset (1973) and Genov (1984). Vaucher (1971) and Vaucher & Durette-Desset (1973) summarize the previous faunistical records of shrew helminths in Finland.

Two infection parameters, *prevalence* (% of hosts infected) and *intensity* (average number of helminths per host), were used to characterize each helminth species. In addition, *total intensity* (average number of individuals of all helminth species per host) and *number of helminth species per host* were used to describe the total helminth burden of shrews. Because females of *Longistriata*-nematodes (two species) could not always be identified to species, the total number of individuals belonging to this genus is given separately in the results.

The helminths tended to exhibit aggregated distributions amongst host individuals (variance markedly greater than mean). Therefore, only non-parametric statistical tests (Kruskal-Wallis', Mann-Whitney's) are used throughout the paper if not otherwise stated.

Similarity of helminth faunas between pairs of host species was assessed using Renkonen's (1938) index (see also Hurlbert 1978). This index is calculated by summing minimums of the relative frequencies of helminth species shared by a pair of host species.

3. Results

3.1. The helminth fauna

Twenty-three species of intestinal helminths belonging to trematodes (4 species), cestodes (14 species) and nematodes (5 species) were found to parasitize the *Sorex* shrews in Finland (Table 1). This helminth community is dominated by cestodes, especially by *Hymenolepis* species.

Two rare species, *Choanotaenia hepatica* and *Dilepis undula*, cannot be regarded as true members of these communities. *Choanotaenia hepatica* normally dwells in the bile duct of its host, but can be found in the small intestine in heavy infections. *Dilepis undula* is a parasite of passerine birds, but occurs accidentally in shrews but is not able to mature in them. The remaining species occur almost exclusively in *Sorex* shrews (all cestodes and some nematodes), or in the shrews of the family Soricidae (all trematodes and some nematodes).

The number of helminth species varied considerably between host species (Table 1). With the exception of the trematode *Rubenstrema opisthiovitellinus* (found only once in *S. caecutiens*), *S. araneus* harboured all of the species in the helminth community (20 species, omitting *C. hepatica* and *D. undula*). *Sorex caecutiens* and *S. minutus* had 12 and 9 species, respectively. The number of helminth species differed significantly between *S. araneus* and the two other shrew species, but not between *S. caecutiens* and *S. minutus* (Table 2).

3.2. Infection levels

Pooled material

Table 1 gives the prevalence and intensity of helminths in the pooled material for the whole of Finland. Five of the species (*H. spinulosa*, *H. schaldybini*, *H. diaphana* (Cestoda), *L. depressa* and *L. pseudodidas* (Nematoda)) occurred commonly in all shrew species. *Sorex caecutiens* and especially *S. minutus* seemed to lack the species which were rare in *S. araneus*, suggesting that the sample sizes were too small for detecting them. On the other hand, there were species which were common in *S. araneus* but occurred only sporadically (*H. scutigera*, *P. winchesi*, *C. crassiscolex*) in the other shrew species (Table 1).

The intensity of most helminth species was highest in *S. araneus* (Table 1), but the intensity of *H.*

Table 1. Prevalences (% of shrews infected) and intensities ($\bar{x}$, geometric mean number of helminths per host) of intestinal helminths in three species of *Sorex* shrews in Finland. X = found only once in the material (*n*=26) which was analyzed for faunistical purposes; – = numbers not counted.

	S. araneus (*n*=51)		*S. caecutiens* (*n*=24)		*S. minutus* (*n*=8)	
	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$
Trematoda						
Brachylaemus fulvus	10	0.1				
Opisthioglyphe sobolevi	12	0.3				
Rubenstrema exasperatum		X				
R. opisthiovitellinus			4	0.04		
Cestoda						
Hymenolepis furcata	14	0.2				
H. spinulosa	18	0.3	13	0.2	25	0.5
H. schaldybini	26	0.6	46	1.7	38	1.1
H. singularis	8	0.1	4	0.1		
H. scutigera	28	0.1	4	0.1		
H. prolifer		X				
H. diaphana	51	6.5	50	2.6	38	1.7
H. tripartita	24	1.2	21	0.7		
H. sp.	12	0.3			13	1.5
H. infirma	4	0.2	8	0.2		
H. globosoides	2	0.03				X
Choanotaenia crassiscolex	37	1.2			13	0.1
C. hepatica	2	–				
Dilepis undula	4	0.03				
Nematoda						
Longistriata pseudodidas	52	1.6	44	0.7	75	1.7
L. depressa	70	4.6	30	0.5	63	0.9
Longistriata spp.(combined)	84	8.9	58	1.6	88	2.2
Capillaria kutori	6	0.1	4	0.03	13	0.3
Parastrongyloides winchesi	35	1.5	4	0.03		
Nematoda sp.	2	0.01				

Table 2. Comparison of the observed and expected (mean ± *SD*, and confidence interval) number of helminth species in *Sorex araneus*, *S. caecutiens* and *S. minutus* (the total number of individuals examined is given in parentheses). The expected numbers are the means of 100 random samples of 8 and 24 individuals, respectively. The confidence interval is the range of values including 95% of observations in the random samples. If the observed number of one species lies outside this range for another species, the two shrew species differ significantly in the number of their helminth species. The analysis is based on 15 common helminth species.

	Obs.	Expected (8)		Expected (24)	
S. araneus (51)	15	11.8±1.7	9–15	14.5±0.8	13–15
S. caecutiens (24)	11	7.1±1.3	4–9	11	
S. minutus (8)	8	8			

schaldybini was relatively higher in *S. caecutiens* and *S. minutus* than in *S. araneus*. The dominance of *H. diaphana* (a cestode) and *L. depressa* (a nematode) in *S. araneus* was striking.

The total intensity and the average number of helminth species per host differed significantly between host species, both parameters being highest in *S. araneus* (Table 3). *Sorex caecutiens* and *S. minutus* did not differ from each other (intensity, P=0.89; number of species, P=0.79).

The quantitative similarity of the helminth faunas did not differ markedly between pairs of shrew species (range 62–67%), suggesting that host specificity does not strongly affect the structure of shrew helminth communities.

Table 3. Infection parameters describing the total helminth burdens of *Sorex* shrews in Finland. The asterisks denote the significance of differences between the shrew species (Kruskal-Wallis' test; *** $P<0.001$, ** $P<0.01$, * $P<0.05$).

	S. araneus		*S. caecutiens*		*S. minutus*	
Sample size						
Pooled material	51		24		8	
Southern Finland	15		–		–	
Eastern Finland	14		10		–	
Northern Finland	22		14		–	
Geom. mean number of helminths per host (range)						
Pooled material (***)	51.0	(0–438)	9.9	(0–79)	10.9	(0–57)
Southern Finland	61.8	(0–373)	–		–	
Eastern Finland (***)	168.0	(23–438)	31.4	(10–79)	–	
Northern Finland (**)	21.0	(0–227)	5.1	(0–64)	–	
Mean number of helminth species per host (range)						
Pooled material (**)	4.2	(0–11)	2.3	(0–9)	2.5	(0–5)
Southern Finland	5.0	(0–8)	–		–	
Eastern Finland (**)	6.4	(4–11)	3.7	(2–6)	–	
Northern Finland (*)	2.2	(0–5)	1.4	(0–4)	–	

Local populations

The helminth communities of *S. araneus* and *S. caecutiens* were compared in two local populations from Lapland and eastern Finland (Fig. 1). Although the dominance relationships of helminths seemed to be roughly similar in both populations, some of the differences between host species were more pronounced in local samples than in the pooled material. For example, in eastern Finland the cestodes *H. furcata*, *H. scutigera* and *Hymenolepis* sp. occurred commonly in *S. araneus*, but were all absent in *S. caecutiens*. The cestode *H. schaldybini* was clearly more common in *S. caecutiens* than in *S. araneus* in both regions.

Both in Lapland and eastern Finland the total intensity and the average number of species per host were significantly higher in *S. araneus* than in *S. caecutiens* (Table 3). Similarly, the total number of species harboured by *S. araneus* (N Finland 8 spp., E Finland 13 spp.) was higher than that harboured by *S. caecutiens* (N Finland 5 spp., E Finland 9 spp.). The quantitative similarity between the helminth faunas of *S. araneus* and *S. caecutiens* was higher in Eastern Finland (69%) than in Lapland (55%).

The three local populations of *S. araneus* differed significantly from each other in total intensity ($P<0.01$) and the average number of helminth species per host ($P<0.01$), both parameters being highest in eastern Finland (Table 3). A similar pattern was observed in *S. caecutiens*. Six of the helminths (*H. schaldybini*, *H. scutigera*, *H. diaphana*, *C. crassiscolex*, *L. pseudodidas* and *L. depressa*) occurred in all three localities. The northernmost locality lacked some of the species which were common in southern areas (*H. furcata*, *H. spinulosa*, *H. tripartita*, *Hymenolepis* sp. and *P. winchesi*).

The weight of shrews varied significantly between the three populations (parametric AOV, $P<0.01$), which may explain some of the observed differences in the respective helminth burdens. The average weight of *S. araneus* was lower in Lapland (6.3±1.0 g) than in eastern (7.6±0.7 g) and southern (7.3±0.6 g) Finland.

4. Helminth communities in other regions

Data on shrew helminth communities were compiled for the following regions: Wales (Lewis 1968), Poland (Soltys 1952, 1954), Bulgaria (Genov 1984), Moldavia (Andrejko 1973), West-Siberia (Judin 1962, Fedorov 1975) and South-Eastern USSR (Baikal district; Eltyshev 1975). These studies were included, because they present quantitative data on

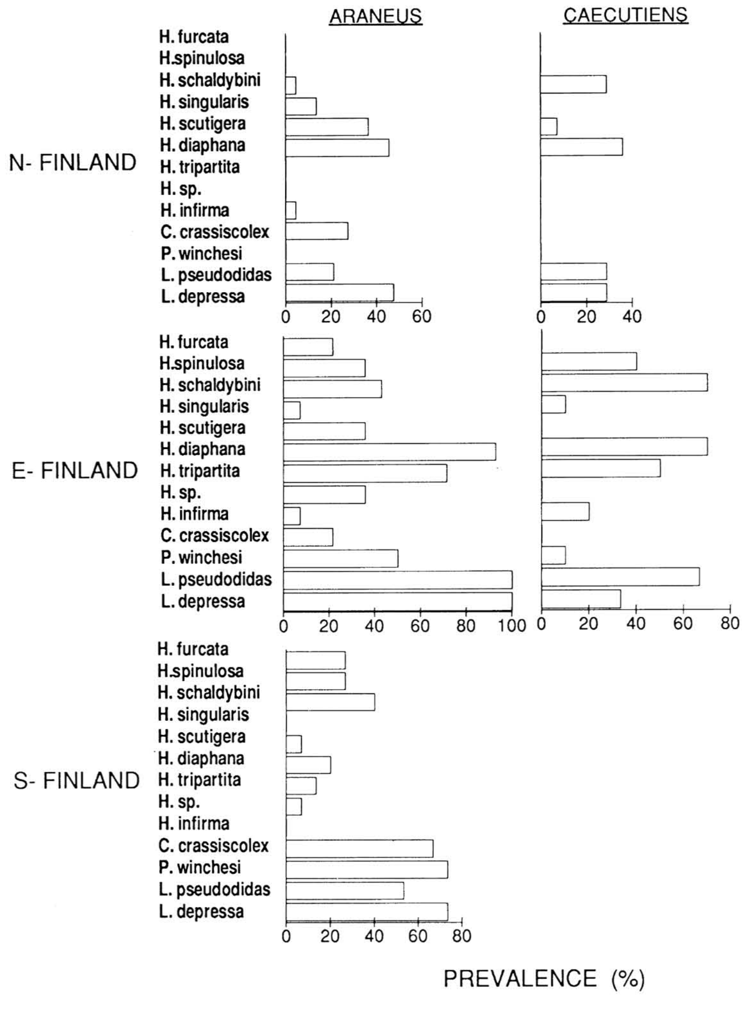

Fig. 1. Prevalences (% of hosts infected) of cestodes and nematodes in the shrews *Sorex araneus* and *Sorex caecutiens* in three regions in Finland. For sample sizes see Table 3.

helminths in at least two species of *Sorex*. Unfortunately, intensities of helminth species were recorded in three studies only, and parameters describing the total helminth burden were not reported.

The total number of helminth species is generally higher in *S. araneus* (all species $\bar{x}$=13.6, common (>1%) species $\bar{x}$=10.4) than in *S. caecutiens* ($\bar{x}$=9.5, $\bar{x}$=8.5) and *S. minutus* ($\bar{x}$=8.9, $\bar{x}$=6.9). This trend was often evident within any one region.

A comparison of prevalences of common helminths between host species did not reveal any consistent patterns; the dominance relationships of helminths are highly variable (Table 4). However, the species *B. fulvus* (a trematode), *H. furcata* and *C. crassiscolex* (cestodes) were almost invariably more prevalent in *S. araneus* than in the other shrew species.

The quantitative similarity of the helminth faunas of *S. araneus* and *S. minutus* was studied using data for the common cestodes and trematodes (species listed in Table 4). The mean overlap between the host species in the same locality was 59% (range 42–85%, *n*=6), while the mean overlap within a host species in different localities was 41% (range 14–80%, *n*=28) in *S. araneus* and 33% (range 0–64%, *n*=22) in *S. minutus*. The overlap between the host species was significantly higher than the overlap within host species in *S. minutus* (*P*=0.01) but not in *S. araneus* (*P*=0.07).

Table 4. Number of helminth species and prevalences of selected helminths of *Sorex* shrews in various geographical regions. *ar* = *S. araneus*, *ca* = *S. caecutiens*, *mi* = *S. minutus*, *arc* = *S. arcticus*, *ro* = *S. roboratus* and *da* = *S. daphaenodon*. *Longistriata* sp. refers to the most common species in that genus. References: Wales, Lewis (1968); Poland, Soltys (1952, 1954); Bulgaria, Genov (1984); West-Siberia, a, Fedorov (1975), b, Judin (1962); South-Eastern USSR, Fltyšev (1975); Moldavia, Andrejko (1973).

	Finland			Wales		Poland			Bulgaria		W-Siberia (a)		W-Siberia (b)						S-E USSR		Moldavia	
	ar	*ca*	*mi*	*ar*	*mi*	*ar*	*ca*	*mi*	*ar*	*mi*	*ar*	*mi*	*ar*	*ro*	*arc*	*ca*	*da*	*mi*	*ar*	*ca*	*ar*	*mi*
Shrews examined	51	24	8	87	43	2439	50	749	619	294	173	21	(Total *n*=321)						110	421	?	?
Helminth species	16	12	9	6	6	12	7	11	21	15	14	9	12	4	5	7	4	3	12	12	16	9
Common (>1%) species	16	12	9	6	6	7	7	4	19	13	9	9	8	4	5	7	4	3	9	8	9	4
B. fulvus	10	0	0	31	12	<1	0	<1	14	5	0	0	0	0	0	0	0	0	0	0	7	0
O. sobolevi	12	0	0	0	0	1	0	0	0	0	71	81	2	0	0	0	8	0	0	<1	0	1
R. exasperatum	0	0	0	0	0	6	8	6	30	21	28	52	26	75	40	35	54	82	0	0	1	0
H. furcata	14	0	0	0	0	<1	0	0	2	0	3	0	18	8	0	3	0	12	0	0	6	0
H. scutigera	27	4	0	21	14	0	0	0	8	7	1	0	0	0	0	0	0	0	3	1	0	0
H. schaldybini	26	46	38	39	42	<1	14	<1	8	19	0	5	0	0	10	6	0	0	10	12	2	0
H. diaphana	51	50	38	0	0	2	4	2	12	6	8	0	<1	0	0	0	0	0	1	2	1	2
C. crassiscolex	37	0	0	33	16	11	6	<1	40	12	18	29	14	8	10	0	0	0	2	0	34	2
Longistriata sp.	70	30	63	0	0	0	0	0	9	2	69	52	3	0	0	0	8	0	3	1	8	3

This result suggests that interspecific patterns in helminth faunas of shrews are not geographically constant (see also Leong & Holmes 1981). Variation between the regions may also be due to the heterogeneity of shrew samples.

In order to examine the occurrence of various types of life-cycles in the helminth communities of shrews, the parasites were classified into three groups: the snail assemblage (species circulating through snails, all trematodes and the cestode *C. crassiscolex*), the insect assemblage (species circulating through insects, hymenolepidid cestodes) and nematodes (direct life-cycles; the life-cycles of some nematodes are unknown).

As expected, the snail and insect assemblages dominated the helminth communities of shrews, except in Finland, where the proportion of the nematode assemblage was high in all shrew species (Fig. 2). Regional variation in the relative frequencies of the three assemblages was parallel in *S. araneus* and *S. minutus* but no other consistent trend between the shrew species or study regions was found. The proportions of species belonging to the different assemblages varied significantly between localities both in *S. araneus* and *S. minutus* (χ^2=319.8, P<0.001 and χ^2=127.4, P<0.001, respectively).

5. Discussion

A dominant feature of shrew helminth communities in Finland is the clear difference in the infection levels between *Sorex araneus* and the other shrew species, *Sorex caecutiens* and *Sorex minutus*. *Sorex araneus* harbours more helminth species, has a higher total intensity and more species per host individual, on average than *S. caecutiens* and *S. minutus*. Taking into account that *S. araneus* is also the dominant shrew species (Hanski 1990), it is evident that the bulk of helminth individuals live in *S. araneus*, the other shrews playing a minor role in their circulation. The following sections attempt to relate the differential infection levels of the shrew species to three factors characterizing the host species.

5.1. Size of shrews

Other things being equal, large species of shrew consuming a large amount of food and having long intestines can be expected to harbour larger populations of helminths than small shrews. The Finnish data clearly support the size-hypothesis. *Sorex araneus*, which has the most diverse helminth fauna, is distinctly larger (this study: $\bar{x}$=7.0 g) than *S. caecutiens* ($\bar{x}$=4.0) and *S. minutus* ($\bar{x}$=2.6), and it has consequently higher food requirement than the other *Sorex* species (Hanski 1984).

In other geographical regions *S. araneus* tends to have more diverse and abundant helminth communities than the smaller shrews, though there is considerable variation amongst the regions. If data were available on infection levels in individual hosts, it is probable that interspecific differences in helminth burdens of shrews would be more visible. The Finnish material shows that despite comparable prevalences of the dominant helminths in different shrew species, the intensities are almost invariably highest in *S. ar-*

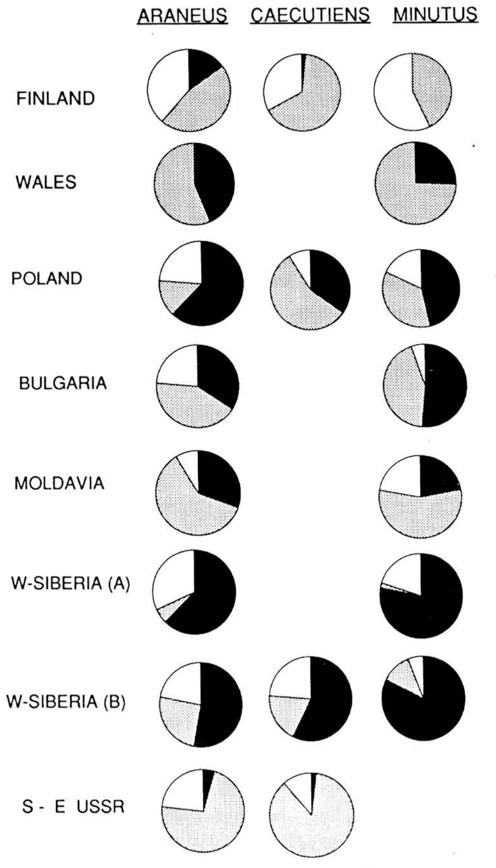

Fig. 2. Proportions of three assemblages of helminths in three species of *Sorex* shrews (*S. araneus*, *S. caecutiens* and *S. minutus*) in different geographical regions. Black = snail assemblage (helminths transmitted in molluscs), shaded = insect assemblage (helminths transmitted in insects) and white = directly transmitted helminths (no intermediate hosts). See text for the species composition of the three assemblages. References as in Table 4.

aneus. Similar results have been reported for *S. araneus* and *S. minutus* in Wales (Lewis 1968), Moldavia (Andrejko 1973) and West-Siberia (Fedorov 1975).

Results on infection levels in small and large species of shrew in the genera *Neomys* and *Crocidura* do not consistently fit the size-hypothesis (Bulgaria; Genov 1984). The large shrews *Neomys fodiens* and *Crocidura leucodon* are characterized by higher prevalences of cestodes (specialists on *Neomys* and *Crocidura*) but lower prevalences of trematodes (generalists) than the smaller species *Neomys anomalus* and *Crocidura suaveolens*.

The extensive material of Judin (1962) on the helminths of seven species of *Sorex* in western Siberia suggests that the large and medium-sized shrews *S. araneus* (13%), *S. roboratus* (13%) and *S. arcticus* (10%) have a higher overall prevalence than the smaller species *S. caecutiens* (6%), *S. minutus* (5%) and *S. minutissimus* (0%). An interesting exception to this pattern was *S. daphaenodon*, a relatively small species harbouring a small number of helminth species but having the highest prevalence (22%) in the shrew community.

5.2. Diet of shrews

Sorex araneus has the most generalized diet amongst the three species of *Sorex* studied in this paper. *Sorex araneus* consumes earthworms more frequently than *S. caecutiens* and *S. minutus*, and it is also able to consume larger food items than the smaller species (Judin 1962, Ivanter 1975, Pernetta 1976, Butterfield et al. 1981). *Sorex araneus* and *S. caecutiens* consume snails and slugs more often than *S. minutus*. The broad diet of *S. araneus* probably contributes to the high helminth diversity in this species.

Differences in diet seem to explain some of the interspecific differences in the occurrence of helminths. The cestode *H. furcata* is transmitted primarily in large copro- and necrophagous beetles, such as *Geotrupes*, *Nicrophorus*, *Oeceoptoma* and *Silpha*, which may explain its absence in smaller shrews. *Hymenolepis schaldybini*, which is often a dominant species in *S. caecutiens* and *S. minutus*, uses smaller beetles, such as *Catops* and *Tachinus*, as its intermediate hosts (for the life-cycles of shrew cestodes see Vaucher 1971).

The helminths which are transmitted by insects, for instance the *Hymenolepis* cestodes, could be expected to predominate in the helminth communities of *S. caecutiens* and *S. minutus*, which mostly feed on small insects. The frequency of the insect assemblage is not, however, consistently higher in the small shrew species than in *S. araneus*.

The use of molluscs by *S. araneus* and *S. caecutiens* is not consistently related to the frequency of the snail assemblage amongst the helminths of different shrew species. The high infection levels of the snail-transmitted helminths *B. fulvus* and *C. crassiscolex* in *S. araneus* could be explained by its food habits, but in some regions (Bulgaria, West-Siberia) the snail assemblage also dominates the helminth community of *S. minutus,* which is believed to use snails only little. The use of earthworms by *S. araneus* cannot explain interspecific differences in helminth burdens, because none of the shrew helminths is known to be transmitted by earthworms.

In summary, the diversity of the helminth community and the frequent occurrence of some helminth species in *S. araneus* may be related to diet. However, interspecific differences in the overall abundance of helminths cannot generally be explained by diet.

5.3. Abundance of shrews

Amongst the parasites that are not strictly host-specific the bulk of the population is generally found in a single host species (Holmes 1983, Holmes et al. 1977). If one of the host species is clearly more abundant than the others, parasites would be expected to adapt to utilize that species most efficiently. Consequently, the relative abundances of the host species are expected to affect the degree of host-specificity in helminths (Holmes 1983).

According to the abundance-hypothesis *S. araneus* harbours many helminth species and has heavy helminth burdens because the helminths have specialized on the most abundant species in the shrew community. This should be the general pattern in Europe and western Siberia, where *S. araneus* dominates the shrew communities.

Sorex minutus is the only *Sorex* species in Ireland, where it has five species of intestinal helminths (Grainger & Fairley 1978). The high infection levels of the cestodes *H. scutigera* and *H. schaldybini* (both specialists on *Sorex*) and the trematode *B. fulvus* indicate that some of the shrew helminths can circulate efficiently in *S. minutus* even in the absence of other, larger and generally more abundant shrew species.

The larvae of *Porrocaecum* nematodes, with birds of prey as their definitive hosts, dwell in extra-intestinal locations in shrews. In northern and eastern Finland, *Porrocaecum* larvae occur distinctly more frequently in *S. araneus* than in the other shrew species, including another large but uncommon species, *S. isodon* (Erkinaro & Heikura 1977). This clearly supports the abundance-hypothesis. Judin's (1962) data indicate that *Porrocaecum* is more prevalent in the large species *S. araneus* and *S. roboratus* than in the smaller species, in agreement with the size-hypothesis.

6. Conclusions

The present analysis suggests that both the size, diet and population density of shrews are likely to contribute to the observed differences in helminth burdens in *Sorex* shrews. Unfortunately, it is hard to disentangle the relative importance of the various factors with these data, because the most heavily parasitized species *S. araneus* is the largest and most abundant and has the most generalized diet among *Sorex* shrews.

Interspecific differences in the helminth communities of shrews showed no clear patterns over large geographical regions. It is however possible that lack of data on total helminth burdens in individual shrews and heterogeneity of shrew samples obscure real differences in the infection levels between different species.

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