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Distribution patterns and microhabitat segregation in gastrointestinal helminths of *Sorex* shrews

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Abstract We studied the distribution patterns and microhabitat use in gastrointestinal helminths of the shrews *Sorex araneus* and *S. caecutiens* in Finland. The distribution of species prevalences was bimodal, and in *S. araneus* the abundance (mean intensity) was positively associated with commonness (prevalence), as assumed by the core-satellite species hypothesis (Hanski 1982). However, the positive correlation between prevalence and intensity was observed only when the effects of helminth body size and taxonomic group (cestodes vs nematodes) on intensity were controlled for. The nematodes of the genus *Longistriata* occurred predictably as core species, whereas the identity of the core cestodes was more variable between host species and regions. Helminth body size and taxonomic group were not related to the degree of aggregation in shrew populations, but helminth body size seemed to explain the differences in the distribution patterns of helminths between shrews and voles. The core species did not show more segregation in microhabitat use than randomly selected species. In fact, the two core nematodes showed largely overlapping intestinal distributions. We conclude that linear intestinal space is not a key resource for shrew nematodes, but it may be for shrew cestodes.

Key words Helminths · Shrews · *Sorex* · Coexistence
Intestinal distribution

Introduction

Spatial distribution patterns can be described by two variables, the proportion of habitat patches or localities occupied and the average number of individuals per occupied patch. Generally these two variables are positively correlated, and regionally common and locally abundant, and regionally rare and locally less abundant species may be distinguished. Although two other combinations of commonness and abundance are possible (rare and abundant species, and common and scarce species), most species fall into these two categories, as assumed by the core-satellite species hypothesis of Hanski (1982). Consequently, the distribution of species regional distributions should be bimodal.

For parasites, the equivalent of the local population is the population in or on a host individual (infrapopulation). Parasite commonness is therefore defined as the proportion of hosts infected (prevalence) and abundance as the mean number of individuals per infected host (mean intensity). Prevalence and mean intensity tend to correlate positively in parasite communities, suggesting a dichotomy into core and satellite species (Bush and Holmes 1986; Stock and Holmes 1987). As predicted by the hypothesis of Hanski (1982), the common and abundant core helminths of some avian hosts have well-segregated niches (Bush and Holmes 1986; Goater and Bush 1988). On the other hand, the analysis by Haukisalmi (1991) of the commonness and rarity of helminths in the bank vole *Clethrionomys glareolus* was in contrast to the above patterns. Prevalence and mean intensity tended to show a *negative* relationship, probably because of the pronounced effect of helminth body size on the mean intensity, and the helminth species could not be categorised into core and satellite species.

The heterogeneous distribution of individuals among habitat patches is a ubiquitous characteristic of animal populations. Typically the bulk of the population dwells in a few favourable patches, while most of the patches remain unoccupied or sparsely occupied. Aggregated distribution of parasites in the host population is thought to result primarily from heterogeneity among host individuals in exposure, susceptibility and defensive capability (Anderson and Gordon 1982). The interspecific differences in distribution pattern of parasites

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have received surprisingly little attention, although similar phenomena have been studied extensively in free-living animals (e.g. Hanski 1982; Taylor et al. 1978, 1980). The only comparative data on helminth aggregation seem to be those of Haukisalmi (1986) on helminths of voles and those of Boag et al. (1992) on nematodes of sheep; the former analysis showed that nematodes are more aggregated than cestodes.

This study characterises the patterns of distribution and abundance and microhabitat use in gastrointestinal helminths of the shrews *Sorex araneus* and *S. caecutiens*. Specifically, we attempt to answer the following questions: (1) Is there a positive correlation between the distribution and abundance of species, and is the distribution of species prevalences bimodal, as assumed by the core-satellite hypothesis (Hanski 1982)? How predictably does a species belong to the core or satellite species? (2) Are the average abundance and degree of aggregation related to the body size and taxonomic group of helminths? (3) Is there segregation in the use of intestinal space among the core species? We compare the observed patterns with those in voles (Haukisalmi and Henttonen 1993a, b), and discuss their implications for coexistence of parasite species.

Materials and methods

Shrews and their habitats

Shrews were obtained from Pallasjärvi in north-western Lapland in Finland (68°03', 24°09'). The material consists of 114 common shrews (*Sorex araneus*) and 105 masked shrews (*S. caecutiens*) trapped in 1988–1990. Shrews were caught from 13 study grids used for monitoring vole populations, situated within an area of ca. 4 km^2. The habitat of all grids was old spruce (*Picea abies*) forest with thick moss layer (Henttonen et al. 1987).

Because live-traps did not contain food for insectivores, shrews were usually found dead (trapping interval was ca. 6 h). Shrews were frozen immediately after trapping. Later, the alimentary tract (=stomach and intestine) of each shrew was removed and studied for helminths under a dissecting microscope. The intestine was studied in ten sections of equal length.

Most of the shrews (*S. araneus*, 78%; *S. caecutiens*, 70%) were obtained between June and October, but a few specimens were caught in midwinter. During summer and autumn both mature (=overwintered) and immature (summer-born) individuals are present in the shrew population; in other seasons the shrew population consists practically of immature shrews only.

Helminths

Parasites could be usually identified directly under the microscope. When necessary, aqueous preparations were processed, and a series of permanent preparations was used for comparison. Identification of parasites was based on the monographs of Genov (1984), Vaucher (1971), Vaucher and Durette-Desset (1973), and Żarnowski (1960). Earlier data on helminth fauna of *Sorex* shrews in Finland have been presented by Vaucher (1971), Vaucher and Durette-Desset (1973), Haukisalmi (1989) and Haukisalmi et al. (1993). *Soricinia* sp., which was represented by immature individuals only and could therefore not be identified, was most likely *S. diaphana* (see Haukisalmi 1989).

The body size of helminths, which is used as one of the possible factors explaining interspecific variation in the mean intensity and degree of aggregation, was calculated as the product of mean length and width of helminths, based on the measurements of 10 individual worms or on published data (shrew helminths, Genov 1984; vole helminths, Tenora et al. 1983, 1985, 1986a, b).

The intestinal distributions were described as the position (1–10) of the median helminth individual of each helminth species in individual shrews.

Statistical methods

For various correlation analyses we calculated Pearson's r. In the analyses of correlation and covariance, the mean intensity (number of helminth individuals per infected host), body size index and aggregation index of helminths were logarithmically transformed, and prevalence (percent of hosts infected) was arcsin $\sqrt{x}$ transformed.

The distribution of helminths in the host population was described by fitting the negative binomial distribution to the observed data (pooled material). If the observed and predicted frequency distributions do not differ significantly (χ^2-test), the helminths are aggregated in the host population. The degree of aggregation in various helminth species was characterised by Lloyd's (1967) index of mean crowding m, which should be largely independent of the sample mean (Schluter 1990). The index m varies from 0 to n (number of shrews); high values of m indicate high aggregation.

To analyse habitat segregation among helminth species, we first calculated the difference between median intestinal positions for each pair of core species. The average pairwise difference for the three core species was then compared with an "expected" average difference, which was obtained by calculating interspecific distance between three species selected randomly from all species; this procedure was repeated 1000 times for each shrew species.

The rarest species (<5%), and the cestode *Dilepis undula*, which is a parasite of birds and does not mature in shrews, were excluded from these analyses. If not otherwise stated, the analyses therefore include 12 and 8 species of helminths in *S. araneus* and *S. caecutiens*, respectively.

Results

Helminths

A total of 17 species of gastrointestinal helminths were found in the material: 4 trematodes, 9 cestodes and 4 nematodes (Table 1). Except for *Brachylaemus fulvus* and *Capillaria* sp., which normally dwell in the stomach, all helminth species are inhabitants of the intestine. *Sorex araneus* and *S. caecutiens* shared all except some of the rarest helminth species.

As shown earlier (Haukisalmi 1989; Haukisalmi et al. 1994), *S. araneus* has more helminth species and significantly higher infection levels of most species than *S. caecutiens* (Table 1). This interspecific difference was most pronounced for the cestodes *C. crassiscolex* and *Hymenolepis scutigera*. *Neoskrjabinolepis schaldybini* was the only species showing higher infection levels in *S. caecutiens*. The prevalence ($r=0.82$, $P<0.001$, $n=17$) and mean intensity ($r=0.69$, $P=0.06$, $n=8$) of various helminth species correlated positively between *S. araneus* and *S. caecutiens* (Table 1), showing that the status of helminths is not markedly affected by the host species.

Table 1 Indices of infection level, aggregation and body size in gastrointestinal helminths of *Sorex araneus* and *S. caecutiens.* If the prevalence or mean intensity differ significantly between the two shrew species (χ^2 and Mann-Whitney test, respectively), the higher value has been indicated by an asterisk. See text for calculation of body size index. (% prevalence, *x* mean number of helminths in infected hosts, *m* Lloyd's index of mean crowding, not presented for the rarest species)

Helminth species	Body size	*S. araneus*				*S. caecutiens*			
		%	*x*	SD	*m*	%	*x*	SD	*m*
Trematoda									
Brachylaemus fulvus	0.68	4	1.0	0.0	–	0	–	–	–
Opisthioglyphe sobolevi	0.13	2	2.0	0.0	–	2	1.0	0.0	–
Rubenstrema opisthioglyphe	3.85	2	23.0	22.0	–	0	–	–	–
Pseudoleuco chloridium soricis	0.50	3	29.0	28.3	–	0	–	–	–
Cestoda									
Choanotaenia crassiscolex	7.00	39*	5.3*	9.4	10.2	3	1.3	0.6	–
Staphylocystis furcata	3.60	5	3.0	4.9	58.9	1	1	–	–
Neoskrjabinolepis schaldybini	1.51	32	6.8	8.0	6.9	46*	11.1*	12.0	4.5
N. singularis	3.66	9	4.9	6.9	29.6	6	6.2	6.5	40.5
Hymenolepis scutigera	0.44	63*	28.6*	30.0	3.3	12	4.0	4.1	13.8
Soricinia sp.	0.34	10*	20.0*	18.4	18.0	5	11.4	16.6	11.7
Insectivorolepis infirma	0.04	26	84.5*	102.1	9.2	28	43.3	71.5	13.2
Dicranotaenia globosoides	18.0	10*	1.8	1.3	9.1	1	1	–	–
Dilepis undula	0.43	10*	1.5	0.7	5.8	0	–	–	–
Nematoda									
Capillaria sp.	0.51	13*	1.0	0.0	0.1	4	1.0	0.0	–
Longistriata depressa	0.11	74*	18.8*	20.0	3.1	51	7.5	6.6	3.2
L. pseudodidas	0.09	70*	9.1*	7.7	2.3	51	5.8	5.7	3.4
Parastrongyloides winchesi	0.08	19*	4.4	3.5	7.2	6	2.7	2.1	20.2

Prevalence and intensity

In *S. araneus*, the mean intensity was related to the body size of helminths ($r = -0.54$, $P = 0.05$), so that the small species showed higher abundance than the larger species (Fig. 1). Because of this body-size effect, the prevalence-intensity relationship was studied using the residuals from the regression of mean intensities on helminth body size, rather than the observed mean intensities. A correlation analysis applied to all helminth species showed a non-significant association between prevalence and corrected intensity ($r = 0.25$, $P = 0.44$; Fig. 2). However, an analysis of covariance using helminth group as a categorical variable and prevalence as a covariate showed that cestodes have higher corrected mean intensity than nematodes ($F = 35.5$, $P < 0.001$) and that intensity is significantly related to prevalence ($F = 14.9$, $P = 0.004$).

In *S. caecutiens*, the effect of helminth body size on intensity was non-significant ($r = -0.20$, $P = 0.63$; Fig. 1). According to the analysis of covariance, the observed mean intensity did not differ between cestodes and nematodes ($F = 3.7$, $P = 0.11$) and intensity was not related to prevalence ($F = 2.2$, $P = 0.20$).

The distribution of helminth species among prevalence classes was bimodal, both shrew species possessing three helminth species that were characterised by considerably higher prevalence than the other species. *Longistriata depressa* and *L. pseudodidas* may be regarded as the core nematodes and *H. scutigera* as the core cestode of *S. araneus.* The distinction between core and satellite species was less obvious in *S. caecutiens*, but the nematodes *Longistriata* spp. and the cestode *N. schaldybini* were distinguished from the other species by their high prevalence (Table 1, Fig. 2).

Degree of aggregation

With the exception of *Capillaria* sp., the data for all helminth species could be fitted to the negative binomial distribution, indicative of aggregated distribution in the host population. The analysis of covariance using prevalence as a covariate (*Capillaria* excluded) did not reveal significant difference in the aggregation index (*m*) between cestodes and nematodes either in *S. araneus* (*m*: $F = 0.5$, $P = 0.50$; prevalence: $F = 16.5$, $P = 0.004$) or *S. caecutiens* (*m*: $F = 0.3$, $P = 0.59$; prevalence: $F = 15.3$, $P = 0.01$). The partial correlations between the body size of helminths and the aggregation index, controlling for the effect of prevalence on *m*, showed a non-significant relationship in *S. araneus* ($r = 0.20$, $P = 0.60$) and *S. caecutiens* ($r = 0.25$, $P = 0.49$).

Intestinal distributions

The observed average difference in the three core species' median intestinal position was 2.0 in both shrew

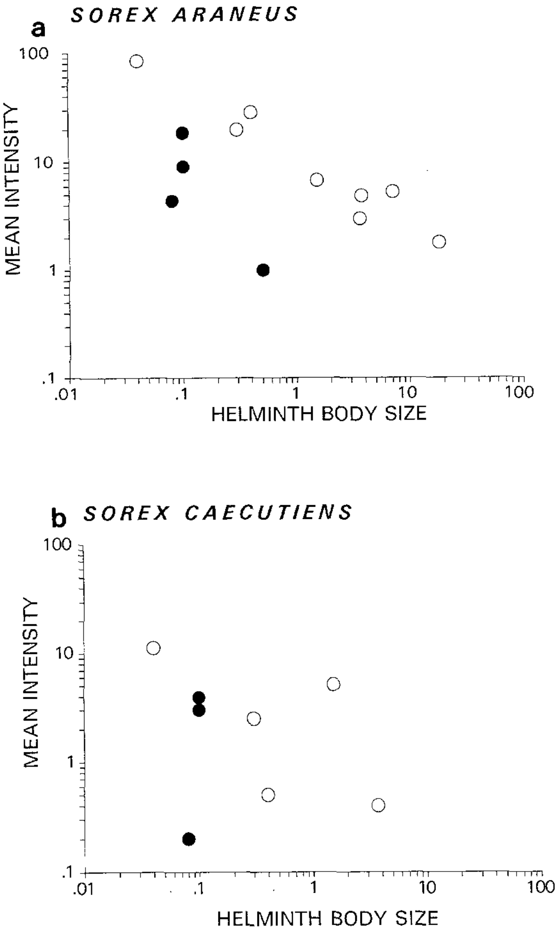

Fig. 1a, b Relationship between body size and mean intensity in helminths of *Sorex araneus* and *S. caecutiens*. (*Open circles* cestodes, *full circles* nematodes)

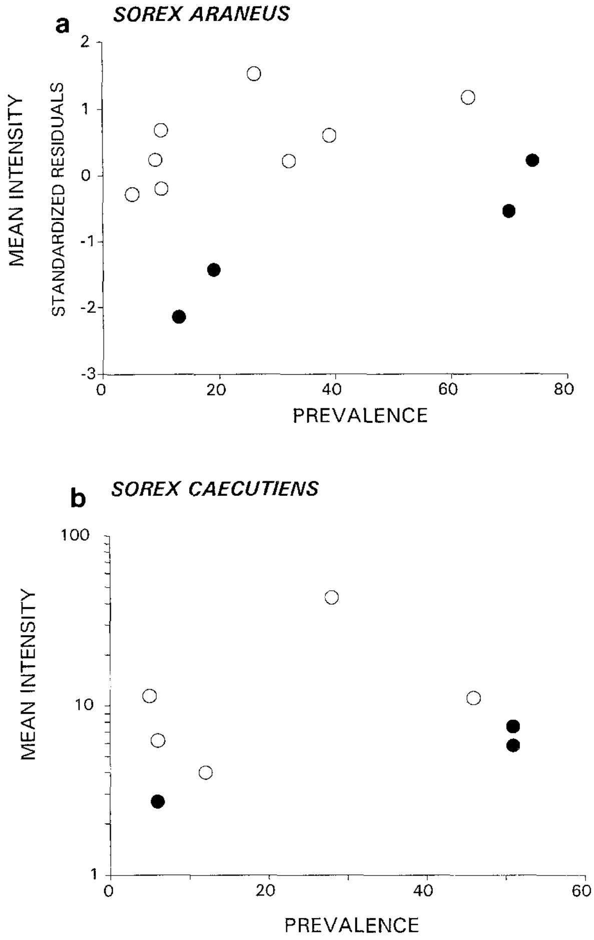

Fig. 2a, b Relationship between prevalence and mean intensity in helminths of *Sorex araneus* and *S. caecutiens*. (*Open circles* cestodes, *full circles* nematodes)

species, which was identical to the expected difference in *S. araneus* ($x = 2.0$, SD = 1.06) and lower (but not significantly so) than the expected difference in *S. caecutiens* ($x = 3.97$, SD = 1.57). The core species' intestinal positions are thus not better spaced out than those of randomly selected species (Fig. 3).

The core nematodes *L. depressa* and *L. pseudodidas* showed largely overlapping intestinal distributions in the anterior intestine of both shrew species. The core cestodes *H. scutigera* (in *S. araneus*) and *N. schaldybini* (in *S. caecutiens*) occupied a more posterior position, which did not overlap markedly with those of *Longistriata* spp. However, these cestodes did not show any segregation in relation to each other (Fig. 3).

Discussion

Core and satellite species

The distribution (prevalence) and abundance (mean intensity corrected for body size) of helminth species were positively associated in *S. araneus*, suggesting a dichotomy into the core species with a high prevalence and high mean intensity and the satellite species with a low prevalence and intensity (Hanski 1982). The positive association between prevalence and intensity was, however, observed only when the helminth group (cestodes and nematodes) was used as a categorical variable; this was due to the higher mean intensity of cestodes compared to nematodes. These data thus suggest that the core-satellite dichotomy should be applied to guilds of similar species, which is a basic assumption of Hanski's (1982) hypothesis. Core-satellite dichotomy was supported by the bimodal distribution of helminth species among prevalence classes.

The absence of a significant prevalence-intensity relationship in *S. caecutiens* may be simply due to the fact that such patterns are hard to observe in an assemblage consisting of a small number of species. Moreover, most of the helminth species circulate primarily through the most abundant host species *S. araneus*, which suggests that all community patterns are likely to be more discernible in *S. araneus* than in the other species of *Sorex*.

The core species consisted of two species of *Longistriata*-nematodes and one species of cestode. A compari-

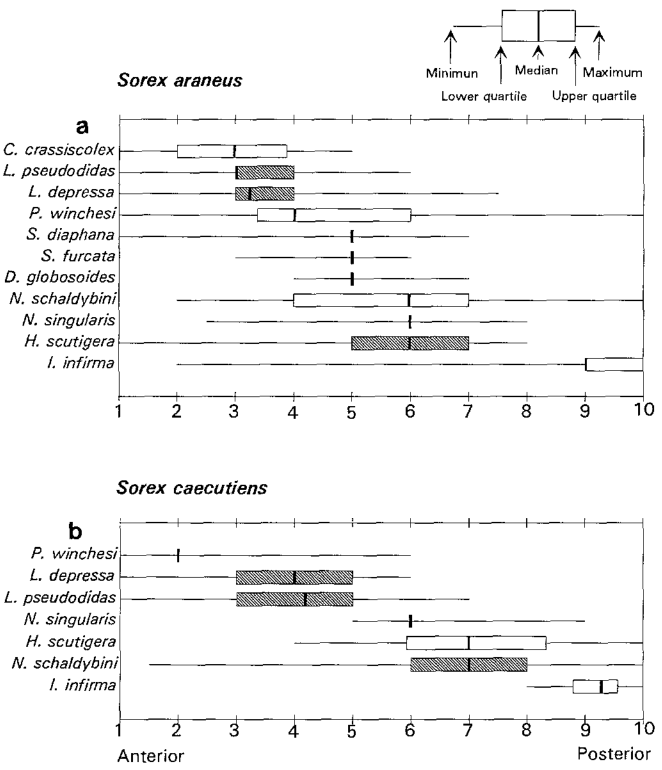

Fig. 3a, b Intestinal distributions of helminths in *Sorex araneus* and *S. caecutiens*, based on the position of the median helminth individual in each infected shrew. (*Shaded bars* core species, *open bars* satellite species; no confidence bars are shown for the rarest species)

son of shrew helminth communities in various localities in Finland (Haukisalmi 1989) shows a similar, predictable structure. According to these data, there is little geographic and interspecific variation in the identity of core nematodes, but the identity of core cestode varies more (three species belonging to different genera have been identified as core cestodes in Finland). A comparable structure also characterises the helminth communities of the bank vole *Clethrionomys glareolus* (Haukisalmi and Henttonen 1993a). An obvious explanation for the variability of the cestode guild is their indirect life-cycles (the intermediate hosts of shrew cestodes belong to a number of invertebrate groups, Vaucher 1971; *Longistriata* have no intermediate hosts). The dominance relationships among cestode species are therefore affected by the abundance and infection dynamics of intermediate hosts, and by the diet of shrews. At a larger spatial scale helminth communities do not show any consistent patterns (Haukisalmi 1989).

Average abundance and aggregation

The negative correlation between helminth body size and intensity suggests that intraspecific competition for food or, more likely, for limited intestinal space is the key factor in the determination of average infrapopulation density of helminth species. High density results in impaired growth, reproduction and survival in helminth infrapopulations (Kennedy 1983). These effects are probably most pronounced for cestodes, which are larger and more abundant than nematodes, and in general more sensitive to intraspecific competition than nematodes. Although the average population size of nematodes is also affected by body size, hosts' immunological mechanisms are thought to play a crucial role in their population regulation (Keymer 1982).

The importance of helminth body size and intraspecific competition is supported by comparisons between host species. *Sorex araneus*, which is a large species with a voluminous intestine, has higher infection levels than the smaller species *S. caecutiens* and *S. minutus* (Haukisalmi 1989). The fact that in this study the clearest interspecific differences were observed in two species of cestode (*Choanotaenia crassiscolex* and *Hymenolepis scutigera*) also supports the role of intraspecific competition for space. The average helminth body size and body size/host length ratio of voles are clearly higher than those of shrews (Table 2). The cestodes of voles are especially large, some species exceeding a length of 20 cm (Tenora et al. 1986a), whereas the largest cestodes of shrews reach a length of 5 cm. Because the large body size of vole cestodes efficiently limits their infrapopulation densities, their mean intensity is considerably lower than that of shrew cestodes.

The degree of aggregation within the shrew popula-

Table 2 Average mean intensity and body size of helminths, and ratio of helminth body size to host body length (cm) in gastrointestinal helminths of shrews and voles. If a helminth species occurred in more than one host species, the helminth-host combination with the highest mean intensity was used. Data for vole helminths are from five host species of the genera *Microtus* and *Clethrionomys* (Haukisalmi 1986)

	No. of species	Mean intensity		Helminth body size		Helminth body size/host length	
		Mean	Range	Mean	Range	Mean	Range
Shrews							
Cestodes	9	17.4	1.5–84.5	3.9	0.04–18.0	0.67	0.01–3.3
Nematodes	4	8.3	1.0–18.8	0.2	0.08–0.5	0.04	0.01–0.09
Voles							
Cestodes	6	1.5	1.1–2.7	116.1	1.7–360.0	9.33	1.7–28.1
Nematodes	5	41.5	3.1–114.0	10.1	0.7–32.6	0.87	0.07–2.7

tion was independent of body size and taxonomic group of helminths. This is an unexpected result, since large body size implies strong intraspecific competition for space and, consequently, fairly uniform distribution of helminths among hosts. For example, large body size seems to explain the absence and low degrees of aggregation in cestodes of voles (Haukisalmi 1986, 1991). Probably the shrew helminths are so small relative to the intestinal space that regulatory effects due to space limitation are not as strong as in vole cestodes (notice the great difference in cestode intensity, body size and body size/host length ratio between voles and shrews, Table 2).

Habitat segregation and coexistence

The median intestinal positions of the core species were not more evenly spaced out than those of randomly selected species, which is in contrast to the predictions of the core-satellite species-hypothesis (Hanski 1982) and earlier results on helminths of waterfowl (Bush and Holmes 1986; Goater and Bush 1988). Why do the helminth communities of shrews lack this expected structure? Helminth communities of waterfowl differ in two respects from those of shrews. First, the avian helminth communities are much more diverse and abundant than the shrew helminth communities, and second, all the core helminths of waterfowl are cestodes, whereas both cestodes and nematodes are included in the core species of shrews. Obviously the space limitation is very severe for waterfowl helminths, which is expected to result in habitat segregation among several co-ocurring species of cestode. Since only one species of core cestode was identified in each shrew species, we can not analyse these patterns among shrew helminths. However, the intestinal positions of the four commonest species of cestode in *S. araneus* indicate a partial microhabitat segregation: one of the species (*C. crassiscolex*) dwells in the anterior intestine, one in the posterior intestine (*Insectivorolepsis infirma*), and two species (*H. scutigera* and *N. schaldybini*) have identical distributions in the mid intestine (Fig. 3). It is interesting that the core cestodes with a similar intestinal position are specialised on different host species. If we assume that intestinal space is the key resource for cestodes, partial host specificity may be a mechanism enhancing their coexistence.

The two core nematodes (*Longistriata*) had largely overlapping intestinal distributions in both shrew species. Since these helminths also show aggregated distributions, positive co-occurrence patterns, synchronous seasonal and annual population dynamics (Haukisalmi and Henttonen, unpubl.) and specialisation on the same host species, their populations overlap strongly. A comparable situation exists between two common nematodes of the bank vole *Clethrionomys glareolus* (Haukisalmi and Henttonen 1993a, b). What promotes the coexistence of these seemingly identical species? An obvious explanation is that the core nematodes are segregating according to a key resource that has not yet been identified. For example, the otherwise similar nematodes may show segregation with respect to the the radial intestinal distribution (lumenal vs. paramucosal distribution; Schad 1963; Bush and Holmes 1986) or the type of food (e.g. epithelial cells, blood, intestinal contents of different particle size). Because of their complete digestive tract and variable mouth-parts, nematodes probably show more feeding specialisation than cestodes, which only can absorb dissolved food (Petter 1962). An alternative view is that coexistence is possible because competitive interactions do not occur between the core nematodes. Ewing and Todd (1961) have shown experimentally that there are mutualistic associations among members of the nematode genus *Metastrongylus* (see also Ewing et al. 1982). Holmes (1973) has suggested that such associations may indicate increased feeding efficiency of the co-occurring species due to diversification of feeding habits. Positive co-occurrence patterns of *Longistriata* species (Haukisalmi and Henttonen, unpubl.) show that their populations do better in concurrent infections than in single-species ones, an indication of a mutualistic association.

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