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Feeding ecology of three sympatric *Sorex* shrew species in montane forests of Slovenia

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Abstract. For the understanding of shrew communities, their coexistence and competition, the knowledge of diet partitioning among sympatric shrew species is crucial. In this study, the trophic niches of three coexisting *Sorex* species: *S. alpinus*, *S. araneus* and *S. minutus* were compared for the first time. Shrews were taken from a montane forest habitat in northern Slovenia (NS). A little known species, *S. alpinus*, fed mostly on Insecta (50 %) and Lumbricidae (25 %), as well as Lithobiomorpha, Araneae and Opiliones. Its diet differed significantly from the diet of *S. araneus* and *S. minutus*. On the other hand, a nearly-perfect trophic niche overlap was found for *S. araneus* and *S. minutus* suggesting their great hindrance of competition for food. For comparison, *S. araneus* from a montane forest habitat in southern Slovenia (SS) was considered. *Sorex araneus* from SS fed on 15 taxa, while the shrew diets in NS habitat were half as diverse. In contrast to previous studies, the nearly-perfect overlap of trophic niches in *S. araneus*-*S. minutus* indicates that in montane forest habitat, otherwise highly competitive shrews can share trophic niches.

Key words: coexistence, trophic niche overlap, *Sorex alpinus*, *S. araneus*, *S. minutus*

Introduction

Shrews are territorial mammals (Pernetta 1976, Hutterer 1990, Croin Michielsen 1991, Rychlik 1998, Churchfield 2002) frequently discussed with respect to various aspects of their spatial and trophic niches as well as competition. Shrew foraging behavior is of particular interest because of their small body size, short starvation time and their need to eat relatively large quantities of food (Hanski 1984, Churchfield 1994). Although they have been shown to be wide-spectrum feeders, use of a few different prey taxa and prey sizes has been reported for different shrew species (Pernetta 1976, Saarikko 1989, Churchfield 1994). Prey differences are often the consequence of interspecific competition. Larger and competitively superior shrew species are usually most abundant in more productive habitats, while smaller species find refuge in less productive habitats or its patches, where they may survive because of their low per capita food requirements (Hanski & Kaikusalo 1989). On the other hand, food heterogeneity and quality may enable the coexistence of many shrew species. Competition

depends on habitat properties, species distribution, size, behavior, temporal and microspatial relationships and the availability of resources (Churchfield 1990, Kirkland 1991, Ford et al. 2006).

In the Alps and Dinarids, three ubiquitous *Sorex* species: the Alpine (*S. alpinus* Schinz, 1837), the common (*S. araneus* Linnaeus, 1758), and the Eurasian pygmy shrew (*S. minutus* Linnaeus, 1766), overlap throughout their distributional ranges (Hausser et al. 1990, Hutterer 1990, Spitzenberger 1990). When comparing body lengths and masses, *S. alpinus* (60–85 mm, 6–13 g) and *S. araneus* (48–87.5 mm, 5–14 g) are of similar size, but a third longer and twice the mass of *S. minutus* (40–68.5 mm, 2.4–6.5 g) (Churchfield 1990, 1991, Hausser et al. 1990, Hutterer 1990, Spitzenberger 1990, Kryštufek 1991, Kryštufek et al. 2011). The ecology of *S. alpinus* has been infrequently studied (Kuviková 1986, Spitzenberger 1990), while that of *S. araneus* and *S. minutus* has been frequently dealt with both individually and in syntopy (e.g., Rudge 1968, Pernetta 1976, Grainger & Fairley 1978, Dickman 1988, Churchfield 1982,

1984a, b, 1990, 1991, 1994, Croin Michielsen 1991, Ellenbroek & Hamburger 1991, Zakharov et al. 1991, Churchfield & Rychlik 2006). *Sorex alpinus* lives in rock and soil fissures and similar hidden microhabitats and collects food by digging (Hutterer 1982, Kuviková 1986), while the other two hunt preferably in grassy patches. *S. alpinus* feeds mostly on Lumbricidae, Gastropoda and Arthropoda (ibid.), *S. araneus* on Lumbricidae and Coleoptera, while *S. minutus* forages predominantly on small Araneae, Opiliones and Coleoptera (Churchfield & Rychlik 2006). All three are opportunistic feeders foraging on various soil-, litter- and surface-dwelling invertebrates (ibid.). So far, the Alpine shrew has not been studied pairwise in coexistence.

In experiments, when alone, *S. minutus* is more surface active than *S. araneus*, and when together, such differences are even more pronounced, although they do not fight for a particular food item (Ellenbroek & Hamburger 1991). This vertical habitat segregation involving *S. araneus*-*S. minutus* starts in summer and intensifies by winter; segregation disappears mainly because of an increase in surface activity in *S. araneus*. Congruently, in lowland syntopic populations, significant differences in diet between the two species have been reported, while no such difference was found when the shrew species lived in comparable habitats individually (Churchfield 1984b, Croin Michielsen 1991). *S. araneus* greatly outnumbers *S. minutus* in productive lowland habitats in Britain and Eurasia (Pernetta 1977, Churchfield et al. 1997), but *S. minutus* is numerically dominant in upland moorlands and blanket bog, where small arthropods are abundant but earthworms are few (Butterfield et al. 1981, Yalden 1981, Shore & Mackenzie 1993). Removal of *S. araneus* from the shared habitat increased the niche breadth of *S. minutus* and its consumption of larger prey as a consequence of a competitive release (Dickman 1988). Such differences in diet can be seen as the consequence of either competition or its lack and are also known in other two-species or multispecies communities, e.g., in *S. araneus*-*S. coronatus* (Neet & Hausser 1990) and *S. fumeus*-*S. hoyi*-*Blarina brevicauda* (Ford et al. 1997). Diet differences are generally understood as indicating specialization with respect to the dominant prey types exploited (Churchfield 1994). On the other hand, very similar foods of *S. cinereus*, *S. longirostris* and *S. hoyi* seem to be highly likely influenced if not caused by competitive exclusion resulting in the main cause of their geographical/ecological separation (Whitaker & Cudmore 1987).

In this study, the diets of syntopic *S. alpinus*-*S. araneus*-*S. minutus* in montane habitats were studied and compared for the first time. Because of differences in habitat selection in *S. alpinus* vs. *S. araneus*-*S. minutus* (Hausser et al. 1990, Hutterer 1990, Spitzenberger 1990), the hypothesis states that trophic niches between *S. alpinus* and *S. araneus*-*S. minutus* do not overlap. On the other hand, in *S. araneus* and *S. minutus* inhabiting the same montane habitat, we hypothesize that their trophic niches would considerably overlap because of hindered competition.

Material and Methods

Shrew stomachs have been obtained from two previous investigations on dynamics and density of invertebrate and small mammal fauna in two montane habitats in Slovenia, carried out in the 1990's (Trilar 1991, Kos et al. 2000, Drovenik 2001, Janžekovič & Čas 2001, Čas 2006), for the habitat quality assessment. Specimens were collected by pitfall trapping in the months without a snow cover from May till October (Trilar 1991, Kos et al. 2000, Drovenik 2001, Janžekovič & Čas 2001, Čas 2006). No shrews were killed for the purpose of this study. The investigation was carried out on Smrekovec Mountain (coordinate centroid 46°27'40" N, 14°46'42" E, mean altitude 1360 m) and Peca Mountain (46°25'21" N, 14°52'43" E, 1375 m) in northern Slovenia (NS). The study area included various beech-fir forest types, owing to past land use and environmental conditions (Čas & Adamič 1998, Čas 2006) at altitudes of 1030-1500 m. Comparative investigations were performed at a 110 km distant Snežnik Mountain (45°34'22" N, 14°24'10" E, 1280 m) in the Dinaric Alps of southern Slovenia (SS) in a site with an allopatric population of *S. araneus*. This habitat comprised beech-fir forest at altitudes of 1150-1350 m (Trilar 1991). The sampling efforts in both areas were comparable. In the NS, *S. minutus* (50 %) and *S. araneus* (46 %) were much more abundant than *S. alpinus* (4 %), which was present exclusively in places with rocky and stony microhabitats (Janžekovič & Čas 2001). In the SS on Snežnik Mountain, only *S. araneus* was found (Trilar 1991). In total, the content of 14 individuals of *S. alpinus* (1 ♂, 13 ♀), 124 of *S. araneus* (59 in the NS: 28 ♂, 31 ♀ and 65 in the SS: 39 ♂, 26 ♀), and 58 of *S. minutus* (26 ♂, 32 ♀) stomachs has been analyzed.

The shrew stomachs preserved in 4 % formalin were dissected, and their contents transposed into 70 % ethanol and inspected for major food remnants. Most frequently small fragments of antennae, legs, elytrae

etc. were found. Numbers of preyed individuals were estimated upon specific structures, like heads, chelicerae etc., which enabled unambiguous counting. After that, the contents were heated in 10 % NaOH at 80 °C for 4 hours to dissolve soft tissues. Chitinous, cellulose and other particles were preserved in 70 % ethanol. These were examined under a Nikon Eclipse E800 compound microscope with a mounted digital Net camera DN100, and processed with Eclipse Net software. The photographed prey remnants were identified by comparison with the invertebrates collected at the same time. The invertebrate lengths were measured to evaluate the prey size.

Data analysis

The differences between the relative frequencies of prey species among the three *Sorex* species were tested using Chi-square tests. The shrew species were tested for distribution randomness of prey size classes with deviations from between size classes using Friedman ANOVA Chi-Square test. The Shannon diversity index, H' , was used for comparison of prey diversity:

$$H' = -\sum_{i=1}^s p_i \ln p_i$$

where p_i is the fraction of individuals belonging to the i^{th} species. Spearman rank correlation, r_s , was used in ranking the correlation in diet composition between the shrew species. The diet niches were compared using the Pianka niche overlap index (Pianka 1973):

$$O_{jk} = O_{kj} = \frac{\sum_{i=1}^n E_{ij} E_{ik}}{\sqrt{\sum_{i=1}^n (E_{ij}^2) \sum_{i=1}^n (E_{ik}^2)}}$$

where O_{jk} is the overlap of species j and k , i is the resource level, n is the number of resource levels, E_{ij} is the proportion of the abundance of the species j in the level i , divided by the number of plots within the level i , and E_{ik} the same within level k . The Sørensen quotient of similarity, QS , was used to compare the presence of prey taxa in the shrew diet:

$$QS = \frac{2j}{a+b} \cdot 100$$

where j is the total number of prey taxa common to a pair of compared shrew species; a is the total number of prey taxa eaten by species a ; and b the total number of prey taxa eaten by species b .

Dietary similarity among shrews was investigated through cluster analysis. An unweighted pairgroup analysis using an arithmetic average (UPGMA) was

performed on the matrix of the Pianka niche overlap index among the shrew species to produce a similarity tree. The program SPSS 19 for Windows and NTSYS 2.20v (Rohlf 2002) were used in these statistical procedures.

Results

In total, 180 animal prey items of 18 taxa were identified (Table 1). While no specimen of *S. alpinus* had an empty stomach, 6.8 % of *S. araneus* and 20.7 % of *S. minutus* in NS, and 29.2 % of *S. araneus* from SS did. Approximately 10 % of undissolved remnants were indeterminable. Nine taxa were eaten by *Sorex* species in NS, whereas 15 were eaten by *S. araneus* from SS. The most frequent prey types in all the three species in both locations were Araneae, Lumbricidae and Coleoptera. Diplopoda, which are abundant potential prey, were completely avoided by all three species. Plant remnants, like rootlets and wood particles, were present only in shrews with one animal prey item or none. Prey diversity was relatively low in both regions. It was very similar in the three NS species and higher in *S. araneus* from SS (Table 1).

The sexes were pooled because the differences between diets were not significant (Chi-Square, $p > 0.05$). There were no significant differences between shrews in prey size classes (ANOVA, Chi-square = 2.76, $p = 0.431$, $df = 3$). Pairwise testing of relative prey frequencies showed that, in the NS, the diet of *S. alpinus* differed significantly from *S. araneus* and *S. minutus*, while there was no significant difference between the last two. Prey frequencies of SS *S. araneus* differed significantly from all the three NS species.

Three measures of dietary similarity showed similar patterns. The diets of the three NS species correlated significantly; while *S. alpinus* vs. *S. araneus* and *S. minutus* showed medium correlation, the correlation between *S. minutus* and *S. araneus* was very strong. Correlations between SS *S. araneus* and all NS species

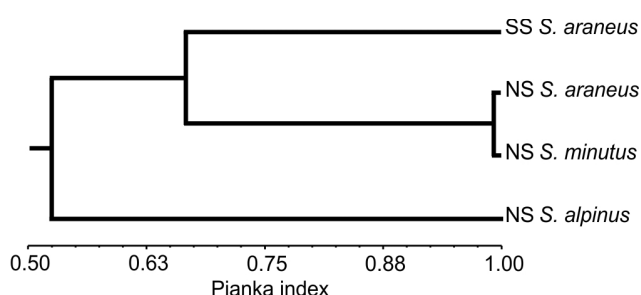


Fig. 1. Comparison of the Pianka niche overlap index between *Sorex araneus*, *S. minutus* and *S. alpinus* in a montane habitat in northern Slovenia (NS), and *S. araneus* in southern Slovenia (SS).

Table 1. Frequency of occurrence (%) of identified invertebrate prey in the diets of *Sorex* species, total number of prey taxa, average number of preyed individuals in shrew stomachs and Shannon diversity index (*H'*). NS – northern Slovenia, SS – southern Slovenia, n – number of specimens.

Prey	<i>S. alpinus</i> NS (n = 14)	<i>S. araneus</i> NS (n = 59)	<i>S. minutus</i> NS (n = 58)	<i>S. araneus</i> SS (n = 65)
Gastropoda (slugs)	0.0	0.0	0.0	6.3
Lumbricidae	25.0	16.4	15.2	17.5
Araneae				
<i>Amaurobius</i> sp.	6.3	29.5	34.8	22.2
Opiliones				
<i>Trogulus nepaeformis</i>	0.0	0.0	0.0	1.6
<i>Lacinius ephippiatus</i>	0.0	0.0	0.0	1.6
<i>Mitopus morio</i>	6.3	11.5	10.9	1.6
Lithobiomorpha	12.5	0.0	0.0	1.6
Insecta indet.	0.0	13.3	13.0	3.2
Coleoptera indet.	6.3	9.8	8.7	1.6
Carabidae indet.	0.0	1.6	0.0	0.0
<i>Aptinus (Aptinus) bombarda</i>	12.5	8.2	6.5	0.0
<i>Nebria dahlia</i>	0.0	0.0	0.0	15.9
<i>Carabus (Megodontus) violaceus</i>	0.0	0.0	0.0	1.6
<i>Philonthus</i> sp.	0.0	0.0	0.0	1.6
<i>Tropiphorus elevatus</i>	18.8	8.2	6.5	3.2
Myrmicidae indet.	0.0	0.0	0.0	1.6
Diptera				
<i>Mikiola fagi</i>	0.0	0.0	0.0	19.0
Dermaptera				
<i>Apterygida media</i>	12.5	1.6	4.3	0.0
n of prey taxa	8.00	9	8	15
n of prey individuals/shrew	1.33	0.96	0.85	0.97
Diversity index (<i>H'</i>)	1.96	1.94	1.87	2.17

Table 2. Prey comparisons between *Sorex araneus*, *S. minutus* and *S. alpinus* in a montane habitat in northern Slovenia (NS), and *S. araneus* in southern Slovenia (SS). c^2 , Chi-Square test; r_s , Spearman rank of correlation; O, Pianka niche overlap index; QS, Sørensen's quotient of similarity.

	<i>S. araneus</i> SS	<i>S. araneus</i> NS	<i>S. minutus</i> NS
<i>S. alpinus</i> NS	$c^2 = 51.03$, $df = 17$, $p < 0.001$ $r_s = 0.04$, $p = 0.877$ $O = 0.44$ QS = 52.17	$c^2 = 41.57$, $df = 17$, $p < 0.001$ $r_s = 0.59$, $p = 0.009$ $O = 0.62$ QS = 82.35	$c^2 = 27.13$, $df = 17$, $p = 0.056$ $r_s = 0.63$, $p = 0.005$ $O = 0.57$ QS = 87.50
<i>S. minutus</i> NS	$c^2 = 67.24$, $df = 17$, $p < 0.001$ $r_s = 0.25$, $p = 0.323$ $O = 0.67$ QS = 52.17	$c^2 = 6.46$, $df = 17$, $p = 0.989$ $r_s = 0.97$, $p < 0.001$ $O = 0.99$ QS = 94.12	
<i>S. araneus</i> NS	$c^2 = 116.73$, $df = 17$, $p < 0.001$ $r_s = 0.16$, $p = 0.537$ $O = 0.66$ QS = 75.00		

were not significant (Table 2). Clustering of the Pianka trophic niche overlap (Table 2, Fig. 1) shows that the diet of *S. alpinus* is unique as compared to the diets of *S. minutus* and *S. araneus* from both regions. Presence of prey species among the NS shrews was very similar – in all NS species, the Sørensen quotient of similarity was over 80 – while between the NS species and SS *S. araneus* it did not exceed 80 (Table 2). In general, differences in prey size among the four shrew groups were very limited (Fig. 2). Although *S. minutus* is considerably smaller than the other two

species, it preyed on animals of similar size as did its congeners. The preferred prey in all three species in both habitats was 6-10 mm long. Prey smaller than 5 mm and longer than 20 mm was also frequently consumed by all the shrews. In *S. araneus* from SS, prey of different size were the most evenly consumed.

Discussion
In this first study on the dietary diversity in sympatric *S. alpinus*, *S. araneus* and *S. minutus* we confirmed considerable differences between *S. alpinus* and

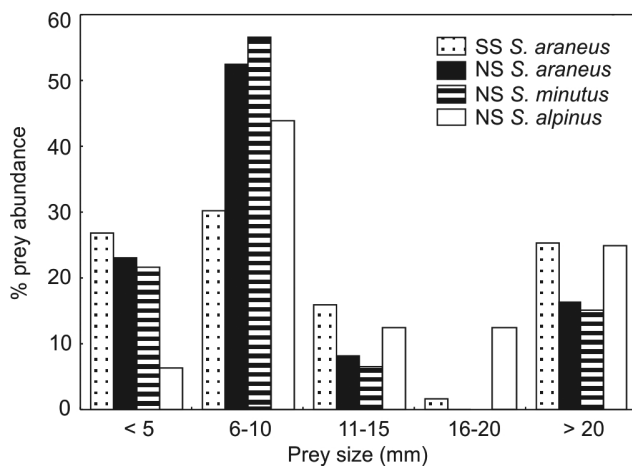


Fig. 2. The occurrence of prey of different sizes in the diet of *Sorex* species.

S. araneus-*S. minutus*. We also confirmed a strong overlap between *S. araneus* and *S. minutus*. This indicated that competition between these two species was strongly hindered as well as that they probably shared the same microhabitat where they encountered the same prey. We therefore speculate that such overlap might have been the result of either the temporal niches partitioning or hindrance of competitive exclusion, or a combination of both, which could be a challenge for further investigations.

Most published pairwise comparisons of shrew diets refer to relatively dense populations in grassland habitats, which could give rise to strong interspecific competition. Usually, smaller shrews in sympatry with larger, competitively superior ones, consume smaller prey, like arthropods, while the large ones eat earthworms. In this way, the smaller shrews narrow their niche breadth and reduce competition (Malmquist 1985, Rychlik 2000, Churchfield 2002). We suggest that in our study the reduction of competition is the consequence of relatively harsh montane forest habitat, with lower temperatures and probably also lower productivity than in lowland habitats.

Churchfield & Rychlik (2006) suggest that body size is the most important promoter of resource partitioning, resulting in different foraging modes. Furthermore, it has been demonstrated that *S. araneus* and *S. minutus* do not differ much in their diet if living alone in comparable habitats (Pernetta 1976), or if their population densities are low (Rudge 1968, Churchfield 1982, Malmquist 1985, Dickman 1988, Churchfield 2002). In our research, differently sized syntopic *S. araneus* and *S. minutus* in NS did not meet these findings, as they evenly shared the prey species pool, probably because the harsh habitat did not favour competition.

As stomachs of all *S. alpinus* were full, it can be suggested that the NS habitat can well supply this species. Both *S. araneus* and *S. minutus* in NS were worse fed, but better than *S. araneus* in SS, where nearly one-third of the specimens had not fed. In accordance with our hypothesis, the diet of *S. alpinus* differed considerably from the diets of sympatric *S. araneus*-*S. minutus* probably because they inhabit different microhabitats and have different feeding habits (cf. Hutterer 1982, Kuviková 1986). Despite 15 prey species in SS *S. araneus* vs. 8 prey species in the NS shrews, their dietary diversities were similar. In SS, this was in particular due to individuals from 1989, when the SS *S. araneus* fed extensively on the dipteran cecidomyid larvae *Mikiola fagi* that were abundant in the SS beech litter in that particular year (Trilar 1991). An appropriate explanation for this is that shrews prefer more profitable prey and are more selective when the encounter rate with such prey is higher (Pearce et al. 1993). On the other hand, the equivalence of the NS *S. minutus* and *S. araneus* diets was due to a very high similarity among the consumed prey taxa and their abundance. It must be mentioned, that H' is most probably underestimated, as only stomachs without intestines were available for the analysis.

In conclusion, the present study provides new information about food partitioning and coexistence in a *S. alpinus*-*S. araneus*-*S. minutus* community of a montane habitat. Their coexistence seems to be possible because of a perfect segregation of trophic niches between *S. alpinus* and *S. araneus*-*S. minutus*, on the one hand, and a great interspecific tolerance between *S. araneus* and *S. minutus* including hindering of competition for food, on the other. In contrast to previous studies this suggests that in harsh conditions, such as montane habitats, spatial and trophic niches of *S. araneus* and *S. minutus* overlap.

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