Diets and coexistence in *Neomys* and *Sorex* shrews in Białowieża Forest, eastern Poland

Sara Churchfield[1] & Leszek Rychlik[2]

[1]Department of Biochemistry, King's College London, 150 Stamford Street, London SE1 9NH, England, e-mail: sara.churchfield@kcl.ac.uk

[2] Mammal Research Institute, Polish Academy of Sciences, 17-230 Białowieża, Poland, e-mail: lrychlik@bison.zbs.bialowieza.pl

Short title for page headings : Diets and coexistence in *Neomys* and *Sorex* shrews

Abstract

Prey selection, food niche overlap and resource partitioning were investigated in semi-aquatic *Neomys fodiens* and *N. anomalus* and terrestrial *Sorex araneus* and *S. minutus* coexisting in marshland in Białowieża Forest, eastern Poland. Evidence of prey selectivity was found but high levels of overlap, particularly in prey size, reflected the abundance of invertebrates in field samples. Despite similarities in diets between all four species, evidence of niche differentiation was found in terms of foraging mode and prey composition. *Neomys* took predominantly terrestrial prey but 20% of prey of *N. fodiens* was aquatic (compared with 11% in *N. anomalus*) with *Asellus* being the dominant aquatic prey. *Sorex* shrews were exclusively terrestrial in foraging mode. All species ate predominantly small prey (≤5 mm) and these were most abundant in field samples, but small prey were most important for *S. minutus*. Pair-wise comparisons suggested that the most important promoter of resource partitioning was body size, indicating different foraging modes. Food niche overlap was least between species most dissimilar in size. The tiny *S. minutus* was predominately an epigeal forager on small Araneae, Opiliones and Coleoptera; the medium-sized *S. araneus* fed extensively on Lumbricidae and Coleoptera; and the large, semi-aquatic *Neomys* fed on different amounts of freshwater prey in addition to terrestrial prey. Our results support the prediction that microhabitat selection among these species indicates differentiation in foraging mode.

Key words: shrews, *Neomys*, *Sorex*, coexistence, diets

INTRODUCTION

Inter-specific competition is thought to be an important force in shaping communities by determining which, and how many, species can coexist. This view is supported by many studies that clearly demonstrate the existence of inter-specific competition (see reviews by Connell, 1983 and Schoener, 1983). The competitive exclusion principle and, more recently, concepts of limiting similarity, optimum similarity and niche packing (Begon, Townsend & Harper, 2005) propose a limit to the similarity of competing species. Several predictions emerge from conventional competition theory: (1) potential competitors that coexist in a community should exhibit differentiation in at least one niche dimension, (2) this niche differentiation should manifest itself in morphological differences between coexisting species and (3) potential competitors with little or no differentiation are unlikely to coexist.

There are situations in which species coexist despite great similarity in morphology and ecology, in apparent contradiction to competition theory. One such example is shrews (Soricidae). Different species of these tiny, insectivorous mammals exhibit high levels of sympatry and syntopy that are likely to bring them into competition for space and resources, accentuated by their particularly high energy requirements (Churchfield, 1990). Moreover, these shrew communities usually comprise congeneric species. A particularly interesting case occurs over much of Europe where two terrestrial species (*Sorex araneus* and *S. minutus*) coexist with two semi-aquatic species (*Neomys fodiens* and *N. anomalus*) (Mitchell-Jones *et al.*, 1999). All four species of shrew can be found coexisting in habitats adjacent to freshwater such as marsh, fen and the banks of water-courses. This provides a model situation for investigating niche differentiation and testing the predictions outlined above. The two terrestrial species have been well-studied, both individually and in syntopy (e.g. Croin Michielsen, 1966; Grainger & Fairley, 1978; Pernetta, 1976; Churchfield, 1982, 1984a,b; Dickman, 1988). Fewer studies have been devoted to the ecology of the relatively elusive water shrews, either singly or in syntopy, and the ecology of *N. anomalus* is particularly poorly known (Dehnel, 1950; Wołk, 1976; Niethammer, 1977, 1978; Kraft & Pleyer, 1978; Illing, Illing & Kraft, 1981; Voesenek & van Bemmel, 1984; Kuvikova, 1985a, 1987; DuPasquier & Cantoni, 1992; Rychlik, 1997). Apart from the work of Kuvikova (1985b) and Rychlik (2000, 2005) no field investigations of niche partitioning have been made of all four of these species living in syntopy.

Two features are predicted to play important roles in differentiation of trophic niches among these shrews, namely foraging mode (terrestrial versus aquatic) and body size. While all four shrews can swim, only *Neomys* species possess adaptations for diving and aquatic foraging (Hutterer & Hürter, 1981; Hutterer, 1985; Ivanter, 1994). Of these, *N. fodiens* is the best-adapted for a semi-aquatic mode of life. Studies suggest that *N. anomalus* is more terrestrial than aquatic in foraging habit (Niethammer, 1977, 1978; Kuvikova, 1987; Rychlik, 1997). Indeed, findings of Rychlik (1997) indicate that *N. anomalus* is a poor diver that does not forage in deep water, unlike *N. fodiens* that can dive deeply to retrieve food (Vogel, Bodmer, Spreng & Aeschimann, 1998). So, *N. anomalus* may be more in competition with terrestrial shrews than with its congenor. However, *N. anomalus* hunted successfully upon aquatic invertebrates and small fish in shallow water, and there were no significant differences between *N. fodiens* and *N. anomalus* in aquatic prey eaten by them in cafeteria tests (Rychlik & Jancewicz, 2002). This suggests that, in the wild, *N. anomalus* eats aquatic prey but it forages in shallow water, providing a basis for niche differentiation between these two *Neomys* species. In a field study of habitat occurrence amongst these shrews (Rychlik, 2000), all four species were found to have high levels of habitat overlap but distance to water and ground wetness appeared to be of significance in niche segregation. This is predicted to reflect differences in foraging mode. Diets and foraging modes are likely to be the most important aspect of niche differentiation in shrews because of their high energy requirements.

Interspecific differences in body size are a useful indicator of (1) behavioural dominance hierarchies that stabilise coexistence of species (Oksanen *et al*., 1979) as well as (2) resource partitioning, particularly in terms of prey size and foraging mode, as has been shown for communities of shrews and other insectivorous mammals (Dickman, 1988; Fisher & Dickman, 1993; Churchfield & Sheftel, 1994; Churchfield *et al*., 1999). *Sorex minutus*, *S. araneus*, *N. anomalus* and *N. fodiens* form a size series, from approximately 3g to 13g in body mass, and this may provide a clue to niche differentiation in areas of syntopy.

The aims of this study were: (1) to examine differentiation in trophic niches of the four mentioned species coexisting in marshland in Białowieża Forest (eastern Poland) with the aim of elucidating the roles of foraging mode and body size in resource partitioning and ecological separation; (2) to verify if differences in microhabitat selection among these species may result from their use of different foraging modes, as predicted in our previous studies (Rychlik 1997, 2000).

METHODS

The study area

The study area occupied 5600 m^2 in the valley of the Narewka river in forest compartment 426 of the Białowieża Forest in eastern Poland. A small stream passed through the plot, with depth ranging from 0.5-30 cm depending upon precipitation. The study area comprised three major habitat types: tussock-sedge swamp (*Caricetum appropinquatae*), streamside alder-ash forest (*Circaeo-Alnetum*) and the ecotone between them with patches of *Filipendula ulmaria*. See Rychlik (2000) for more details.

Trapping the shrews

Three 10-day trapping sessions of shrews were performed between 24 June and 27 August 1996 using wooden-box live-traps. The study area was covered with 180 traps distributed in a grid 5 × 5 m (15 rows of 12 traps each). To help minimise 'trap addiction' and facilitate collection of natural, uncontaminated diet samples from trapped shrews, no bait was provided. The traps were left open throughout day and night and, to prevent mortalities, they were inspected every 4-5 hours. The species, age class, body mass and point of capture of each trapped shrew were recorded, and shrews were released at the point of capture. Faecal pellets from each trapped shrew were removed from the trap and placed in individually-marked vials containing 70% alcohol for subsequent analysis of prey remains.

Prey abundance

To assess the availability of prey of different taxa and sizes in the study area, terrestrial and aquatic invertebrates were sampled monthly between June-August 1996. During each shrew-trapping session, 40 pitfall traps (height 100 mm and diameter 55 mm) containing ethylene glycol and few drops of detergent (to reduce surface tension) were set for 7 days to sample terrestrial invertebrates. The traps were distributed in four lines (one in the sedge swamp, one in the forest and two in the ecotone), each with 10 traps placed 2.5 m apart. The pitfalls were covered with wire net (of 8 mm mesh) to prevent small mammals from falling in. Invertebrates active on the ground surface, including most arthropods and molluscs, are well-represented in pitfall traps but this sampling technique does not adequately reflect the abundance of soil-dwelling invertebrates, especially lumbricids and some Diptera larvae (Churchfield, 1982). Logistic and habitat conservation reasons precluded alternative sampling techniques and so data on these invertebrates have to be interpreted with caution.

Benthic invertebrates in the stream were sampled by kicking the substratum and sweeping a pond-net (diameter at net mouth 200 mm, net mesh 1 mm) amongst the submerged plants and muddy substratum. Benthic sampling was performed once per shrew-trapping period, around midday. A sample of benthos was collected at approximately 5 m intervals, resulting in 15-18 samples per sampling session. Benthos was rinsed with water on a 1-mm sieve, extracted from the debris and preserved in 70% alcohol.

Both terrestrial and aquatic invertebrates were identified and placed into size classes (5-mm intervals of body length). For comparative purposes, results were expressed in terms of the relative abundance (%) of prey in different taxa and size classes.

Diet analysis

Dietary analysis was based on microscopic examination of faecal pellets collected from live-traps in which the shrews were caught. The number of faecal pellets produced per shrew varied but a single sample comprised a minimum of three faecal pellets. Only four faecal samples were collected from *S. minutus*. Despite frequent trap inspections, nine captured *S. minutus* died and so their stomachs were examined for prey remains, thereby increasing the number of diet samples of this species. Identification was facilitated by use of a reference collection of potential prey items taken from the study area. Comparison of the invertebrate prey remains with the reference collection permitted the prey to be categorised according to their body size.

The results were expressed as follows: the percentage frequency of occurrence of food items (the proportion of specimens containing a named food type), the percentage dietary occurrence of food items (the number of occurrences of a named food type as a proportion of the total occurrences of all food type), and the percentage volume composition of each food type (estimated by comparing the sizes of food remains with whole specimens in the reference collection). An index of the contribution of each food type was derived which incorporated the latter two measures:

$$\text{\% dietary composition} = \frac{\text{\% dietary occurrence} + \text{\% volume composition}}{2}$$

To compare the diets of shrews, the following indices of niche breadth and niche overlap were used:

$$\text{Diversity Index } H' = -\sum pi \log_e (pi)$$

where *pi*= the proportion of each prey type in the diet.

$$\text{Sorensen's Quotient of Similarity } (QS) = \frac{2j}{a + b} \times 100$$

where *j*= total number of prey taxa common to the two shrew species being compared, *a*= number of prey taxa found in species a, *b*= number of prey taxa found in species b.

Dietary overlap (after Pianka, 1973): $O_{ab} = \dfrac{\sum p_{ia}\, p_{ib}}{\sqrt{\sum p^2_{ia}\, p^2_{ib}}} \times 100$

where O_{ab} = mutual overlap between shrew species a and b; p_{ia} = proportion of resource used by species a; p_{ib} = proportion of resource used by species b.

Where the numbers of samples were comparable for statistical analyses the *G*-test (with William's correction) using the χ^2 distribution (Fowler & Cohen, 1995) and 'Student's' *t*-test were used.

RESULTS

Number of samples examined and validation of the technique

Fig. 1 shows the cumulative percentages of different prey taxa found as increasing numbers of samples were examined. Fig. 1a suggests that sufficient samples of *S. araneus* and *N. fodiens* (n= 30 each) were examined to fully represent the diets of these species. Fewer samples were collected from *N. anomalus* (n= 13) yet it can be seen in Fig. 1b that 100% of prey taxa had been found by the tenth sample examined. For *S. minutus* only four faecal samples were available, additional data being obtained from stomachs. Eighty-two percent of prey taxa were found in the scat samples, the rest being found in stomachs, and all prey taxa were discovered by the 10th sample (Fig. 1b). It is concluded that sufficient numbers of samples were examined to be representative of the diets of all four shrew species.

All diet samples contained identifiable remains. For *N. fodiens*, *N. anomalus* and *S. araneus*, the total numbers of different prey types identified were 25, 25 and 21, respectively. Mean numbers of prey types found per faecal sample were 5.4 (range 2-9), 7.7 (range 4-9) and 4.8 (range 2-9) for *N. fodiens*, *N. anomalus* and *S. araneus*, respectively. For *S. minutus*, a mean of 6.8 and 3.7 prey taxa per sample were identified in faeces and stomachs, respectively. A total of 17 different prey types were found in this shrew, and examination of stomachs produced only three additional prey types. Data for both faeces and stomachs were combined for subsequent data analyses.

Prey consumption and selection

The frequency of occurrence of different prey taxa identified in the diets of the four shrew species is shown in Table 1 and the dietary composition of major prey in Fig. 2. All species ate a wide range of invertebrates but no vertebrate remains were found. *N. fodiens* and *N. anomalus* ate both terrestrial and aquatic prey but the two *Sorex* species took only terrestrial prey. Plant fragments were occasionally found in small amounts but, on closer examination, these appear to have been ingested as shrews nibbled on the wooden walls of the traps during their confinement and so they were excluded from the analysis.

Mollusca were eaten by *Sorex araneus* and *Neomys* species. In the case of *Neomys*, these prey could have been of terrestrial or aquatic origin. Where samples contained only remains of the radula and no shell fragments, it was assumed that these were gastropod slugs of terrestrial origin. But, for those containing shell fragments it was not possible to determine their habitat origin since both terrestrial and freshwater snails and bivalves were present in the study area, so these are categorised separately in Table 1 and Fig. 2. As a consequence of their aquatic plus terrestrial foraging, *Neomys* had a higher diversity (*H'*) of food items than *Sorex* (see Table 1).

Both *Neomys* species ate a similar diversity of terrestrial items but Lumbricidae formed a much greater proportion of the diet in *N. anomalus* than *N. fodiens* while

Diplopoda showed the reverse trend (Table 1 and Fig. 2). *N. fodiens* ate a wider range of aquatic prey and consumed a larger proportion of *Asellus* than did *N. anomalus* (Table 1 and Fig. 2). Although both species demonstrated aquatic and terrestrial foraging they subsisted mostly on terrestrial prey. These comprised 75.2% and 82.8% dietary composition in *N. fodiens* and *N. anomalus*, respectively (excluding Molluscs of unknown origin). Moreover, significantly more terrestrial than aquatic prey were eaten per shrew (*N. fodiens*: mean 4.0 terrestrial items, 1.1 aquatic, $t = 6.12$, $p < 0.001$; *N. anomalus*: mean 5.8 terrestrial items, 0.9 aquatic, $t = 6.97$, $p < 0.001$). In terms of dietary composition, 20.3% of the diet of *N. fodiens* but only 11.0% of *N. anomalus* comprised known aquatic prey. While all individuals of both species had eaten terrestrial prey items, only 46.2% of *N. anomalus* faecal samples (compared with 64.5% of *N. fodiens*) contained aquatic items.

S. araneus and *S. minutus* consumed a similar diversity of terrestrial prey but the major differences between the two species were the large proportions of Araneae and Opiliones eaten by *S. minutus* and Lumbricidae taken by *S. araneus* (Table 1 and Fig. 2). Of note were three incidences of *S. minutus* eating earthworms. Coleoptera were a major prey item for all four shrew species.

Apart from aquatic foraging there were differences in the occurrence of certain terrestrial prey in the diets of *Neomys* and *Sorex*. Diplopoda were particularly prominent in *N. fodiens* (less so in *N. anomalus*) but rarely if ever eaten by *Sorex* (Table 1 and Fig 2). Both Diplopoda and Araneae were eaten by significantly more individuals of *N. fodiens* than *S. araneus* (Diplopoda: $G = 19.48$, $p < 0.001$, n= 30; Araneae: $G = 12.12$, $p < 0.001$, n= 30). Lumbricidae were the dominant prey of the three largest shrews (Table 1 and Fig 2) but were eaten by more individuals of *S. araneus* than *N. fodiens* (G= 3.96, p< 0.05, n= 30).

Certain terrestrial prey were eaten by shrews in greater proportions than their abundance in pitfall samples would predict (Fig. 2). All shrews (particularly *S. minutus*) showed selection for Coleoptera, Araneae and Opiliones. Selection for Heteroptera and Lepidoptera was indicated by *Sorex*. *Neomys* (particularly *N. fodiens*) showed selection for Diplopoda while these were avoided by *S. minutus*. Others were taken less frequently than predicted by their abundance in invertebrate samples, such as Diptera adults and Collembola. Certain prey were not adequately sampled by pitfall traps (notably soil-dwelling Diptera larvae and Lumbricidae) and so selection could not be implied.

The most abundant aquatic invertebrates were Chironomidae larvae (Diptera). These small larvae seemed to be avoided by water shrews because they were not found in their diets. Possibly they were too small or too well camouflaged in the muddy substratum to be captured. In contrast, many larger Diptera larvae (including Stratiomyidae and Ptychopteridae) were eaten though they were rare in field samples, suggesting selection for these prey. Selection for Trichoptera larvae is also implied since they were eaten by *Neomys* but were absent from field samples. The only invertebrates found in field samples but not in shrew diets were Homoptera, Hymenoptera (other than Formicidae) and aquatic Hirudinea, but these comprised only small proportions (<1.7%) of the invertebrate fauna.

Body mass and prey size utilisation

These coexisting shrews exhibit differences in body dimension and mass which were predicted to influence the size of prey eaten. The mean body masses of each species captured in the study plot during this investigation were: *N. fodiens* 12.5g (n= 54), and *N. anomalus* 8.0g (n= 13), *S. araneus* 7.2g (n= 85) and *S. minutus* 3.0g (n= 7). Note that these measures comprised mostly juvenile/sub-adult shrews that formed the bulk of the trapped population. With the assistance of a reference collection of invertebrates, examination of fragments in scats permitted prey to be categorised according to their lengths.

The dietary composition of prey of different size categories is shown in Fig. 3. Despite their differences in body size, all shrews took mostly small prey. With the exception of *N. anomalus*, all species ate significantly more small prey (≤5 mm) than large prey (≤16 mm): *N. fodiens* $G = 17.46$, $p < 0.01$; *S. araneus* $G = 4.81$, $p < 0.05$; *S. minutus* $G = 16.3$, $p < 0.001$. Nevertheless, the small shrew species took more prey of ≤5 mm than did larger species ($r = -0.916$, $p < 0.05$).

The proportions of prey of different sizes eaten by shrews generally reflected their abundance in field samples, particularly terrestrial invertebrates (Fig. 3). Terrestrial invertebrates of 1-5 mm in body length were by far the most abundant in pitfall samples and these were eaten in the greatest numbers by all shrew species. Medium prey (11-15 mm) were taken in larger proportions by *Neomys* than their abundance in field samples would predict, suggesting selection for these prey. Large invertebrates (>20 mm) were also taken in bigger proportions by *Neomys* and *S. araneus* than expected. However, this probably reflects the inadequacy of pitfall traps in sampling the larger soil-dwelling invertebrates such as earthworms and larger dipteran larvae.

Dietary overlap

Indices of dietary overlap in the different food niche dimensions are compared in Table 2. In pair-wise comparisons, highest overlaps occurred with respect to prey size, emphasising the importance of small prey even to the larger species. This is not surprising since small prey were the most abundant in invertebrate samples (Fig. 2). Overlap in all dimensions was generally greatest between the two semi-aquatic *Neomys* species. There was greater similarity in their terrestrial feeding habits (O_{ab} = 86.2% for dietary composition) than their aquatic foraging (O_{ab} = 70.3%).

Dietary overlap between the two terrestrial *Sorex* species was high in terms of shared prey (Table 2) but lower in terms of dietary composition and prey size. The difference was primarily due to the large proportions of tiny Araneae eaten by *S. minutus* and larger Lumbricidae consumed by *S.araneus*.

In pair-wise comparisons, dietary overlap in prey composition was negatively correlated with the ratio of shrew body mass (Fig. 4) suggesting resource partitioning by shrews on the basis of body size. The most similar pairs (in size and morphology) were *N. anomalus* and *S. araneus,* and *N. fodiens* and *N. anomalus,* and they had the greatest overlap. Least similar were *N. fodiens* and *S. minutus* with overlap of just 44%.

DISCUSSION

Methodological considerations

Diets of small insectivores deduced from faecal analysis have been criticised for a number of reasons. It is often thought that 'soft' parts of invertebrates cannot be detected and are thereby unwittingly excluded. But, even Diptera larvae leave identifiable remains (see Table 1). Use of the scat analysis technique for insectivorous mammals has been reviewed and its value clearly demonstrated in a variety of studies (Churchfield, 1982, 1984a; Dickman & Huang, 1988). Moreover, the technique is widely used and accepted in the study of larger mammals such as mustelids (e.g. Lodé, 1993, Somers & Purves, 1996; Ebensperger & Bottomahan, 1997; Zalewski, 2004 and papers cited therein). For elusive or rare species (such as *N. anomalus*), faecal analysis is to be encouraged for the quality of data it can produce, its compatibility with population studies based on live-trapping and mark-recapture, and its conservation value (compared with stomach analysis from kill-trapped animals).

One possible omission in the present study is freshwater Hirudinea in the diet of *Neomys*. Small numbers of these prey occurred in field samples (comprising 0.7% of all aquatic prey). To date, the authors have not found a means of identifying remains of these prey in scats but neither have they been reported in stomach analyses from kill-trapping. Indeed, the few published studies of scat analysis and stomach analyses of *N. fodiens* (e.g. Niethammer, 1978; Churchfield, 1984a; Kuvikova, 1985a, b, 1987; DuPasquier & Cantoni, 1992; Castién, 1995) provide good concordance between the two methods. There are more studies of feeding habits of *S. araneus* and *S. minutus* based on stomach and scat analyses (e.g. Rudge, 1968; Pernetta, 1976; Grainger & Fairley, 1978; Churchfield, 1982, 1984a; Churchfield & Sheftel, 1994). Comparison of their findings also supports the viability of faecal analysis.

Dietary composition of shrews

Other diet studies of *S. araneus* and *S. minutus* have shown a wide range of prey items being eaten, similar to those found in our study (Rudge, 1968; Pernetta, 1976; Churchfield, 1982, 1984a; Kuvikova, 1985b; Churchfield & Sheftel, 1994). All confirm that *S. araneus* is a major consumer of Oligochaeta and Coleoptera while *S. minutus* eats large numbers of Araneae, Opiliones, Coleoptera and sometimes Isopoda. In contrast to other studies, we found just three incidences of *S. minutus* having eaten earthworms, a most unusual finding. In our study it appears that, while Coleoptera are eaten in similar proportions by both *Sorex* species, Lumbricidae is the main food resource for *S. araneus* while Araneae plus Opiliones are the principal food for *S. minutus*. The dietary overlap between these two species in terms of shared prey (82%) was very similar to that recorded by Churchfield (1984a) and Churchfield & Sheftel (1994), but higher in terms of dietary composition (67% versus 56-57%).

Our investigation found a range of terrestrial and aquatic items in the diets of *N. fodiens* comparable with those of previous studies using stomach and scat analyses (Niethammer, 1977, 1978; Churchfield, 1984a; Kuvikova, 1985a, 1987; Du Pasquier & Cantoni 1992; Castién, 1995, Castién & Gosálbez, 1999). Diplopoda and Oligochaeta have featured in diets of *Neomys* in most of these studies, although not in such large amounts as were recorded here. The absence of Diplopoda from the diet of wild *S. araneus* and their distaste for them in laboratory trials was attributed to the production of acrid secretions by these invertebrates (Rudge 1968). It is interesting to note how important this prey is in the diets of the larger *Neomys* species. There was evidence of selection for these prey, at least by *N. fodiens*, since they were eaten in much greater proportions than their abundance in field samples would predict. Unlike Wołk (1976) and Kraft & Pleyer (1978) we found no evidence of fish and amphibians in the diet of *N. fodiens*.

The main difference between studies is the proportion of aquatic to terrestrial prey in the diets of *N. fodiens*. All confirm that both types of prey are eaten by *N. fodiens* but Niethammer (1977, 1978) and DuPasquier & Cantoni (1992) found that aquatic prey greatly outnumbered terrestrial prey (>70%). Churchfield (1984a), Kuvikova (1985a) and Castién (1995) found aquatic prey comprised only 28-67% of the diet of this shrew, more comparable with the findings of our study (20%). However, there is some evidence that the amount of aquatic foraging may vary with season, habitat and the availability of terrestrial versus aquatic prey. The incidence of aquatic prey in the diet was high in all seasons in the stream-side habitat in the Swiss Alps occupied by *N. fodiens* (DuPasquier & Cantoni, 1992) but Castién (1995) found some evidence that aquatic prey were taken most in spring and least in summer along stream-sides in the Pyrenees (but sample sizes were small). In a Slovak alder forest, no aquatic prey was found in the diet of *N. fodiens* in summer, and in autumn aquatic invertebrates comprised no more than 11% of its diet (Kuvikova, 1985b). Churchfield (1984a, 1998) found a mid-summer decline in availability of some aquatic prey was compensated for by an increase in foraging on the many terrestrial invertebrates that were particularly abundant in summer. This may account for the relatively low level of aquatic foraging by *Neomys* in the present study (summer) since terrestrial prey may be energetically more profitable in terms of encounter rate and ease of capture compared with diving for aquatic prey (Spitzenberger, 1990; Churchfield, 1998). However, the situation is far from clear since Niethammer (1977, 1978) found the proportion of aquatic prey eaten peaked in summer. He also found that the incidence of aquatic prey varied from year to year, with more terrestrial prey being eaten by both *N. fodiens* and *N. anomalus* in drier years (although his sample numbers were small). Conditions during our summer study started with a wet June becoming progressively drier in July and August but the stream retained enough water for aquatic foraging in June and July.

There have been very few studies of *N. anomalus* and so there is little basis for comparison. Kuvikova (1987) examined stomach contents of this shrew from various sites in Slovakia. As with the present study she found a wide range of terrestrial and aquatic prey were eaten, including some Diplopoda and Oligochaeta, but aquatic prey comprised only a small proportion of the diet (around 17%). However, no aquatic prey were reported in the diet of *N. anomalus* in an alder forest in Slovakia (Kuvikova, 1985b) and different habitats in Portugal (Ramalhinho, 1995). Niethammer (1977, 1978) analysed stomach contents of *N. fodiens* and *N. anomalus* living along a brook in the Austrian Alps and found great similarities in the type of prey taken by these shrews. Both ate large numbers of aquatic Diptera larvae and Plecoptera nymphs but *N. fodiens* tended to eat more aquatic prey than *N. anomalus*. This is confirmed in our study, with aquatic prey comprising only 11% of the diet of *N. anomalus* compared with 20% in *N. fodiens*. Although the proportions of aquatic prey eaten by *N. fodiens* may vary with site, season and even year, evidence is compelling that it is more aquatic in foraging mode than is *N. anomalus*.

Prey size utilisation

The high incidence of small prey (particularly terrestrial invertebrates) being eaten by all shrew species in this study, irrespective of the shrew body size, probably reflects their great abundance, as indicated by field samples. This is supported by Churchfield *et al.* (1997) who found that prey of 3-5 mm in length were significantly more abundant than larger prey in most terrestrial habitats in Siberian taiga.

Castién & Gosálbez (1999) also found great overlap in prey size taken by co-existing shrews in the Pyrenees, even though the mean length of prey was larger than in the present study (9 mm for *N. fodiens* and *S. minutus*, 13 mm for *S. araneus*). In common with our study, the greatest size differences in prey corresponded with the different amounts of Lumbricidae consumed. In our study the size of shrew was negatively correlated with the occurrence of small prey (≤5 mm), with very small prey being particularly important to the tiny *S. minutus*.

Niche overlap and resource partitioning

As predicted, we found evidence of niche differentiation in these coexisting shrews that were based on their morphological differences (in body size and adaptations to aquatic foraging), but the trophic differences between them were smaller than expected. Despite the adaptations of *Neomys* for aquatic foraging, most of their prey comprised terrestrial invertebrates, resulting in overlap with the terrestrial *Sorex*. Indeed, the greatest overlap, in terms of dietary composition, occurred between *N. anomalus* and *S. araneus*. There was some differentiation between *Neomys* in the amounts of aquatic prey eaten by the two species. Despite elements of high food niche overlap between shrews in our study, pair-wise comparisons suggested that, apart from aquatic/terrestrial foraging modes, the most important promoter of resource partitioning was body size. Overlap was smallest between species with the greatest size differences equipping them for different foraging modes. The tiny *S. minutus* was predominately an epigeal forager on small Araneae, Opiliones and Coleoptera; the medium-sized *S. araneus* was more hypogeal, feeding extensively on soil-dwelling Lumbricidae; and the large, semi-aquatic *Neomys* dived or waded for different amounts of freshwater prey in addition to terrestrial prey. This supports other studies (Dickman, 1988; Fisher & Dickman, 1993; Churchfield & Sheftel, 1994; Churchfield *et al.,* 1999) that have shown that differences in body size amongst coexisting insectivorous mammals promotes ecological separation. Our results also support the prediction that microhabitat selection among these species, as observed by Rychlik (2000), indicates differentiation in foraging mode.

Why were food niches of *Neomys* and *Sorex* not more distinct? Our study was limited to a single season (summer) which may not provide a full picture of food niche overlap and resource partitioning amongst the shrews studied. Competition for food may be greater in cold, northern temperate winters when terrestrial invertebrates are less numerous, less active and less accessible due to low temperatures and frozen soil (Näsmark, 1964; Aitchison, 1978, 1979a,b; Churchfield, 2002). However, winter is also the time of minimum population densities of shrews (Borowski & Dehnel, 1952; Mezherin, 1960; Churchfield, 1980, 1984b). Our study was conducted during the summer peak in shrew numbers when breeding takes place and competition for resources is predicted to be high. In their study of coexisting shrews, moles and desmans in the Spanish Pyrenees, Castién & Gosálbez (1999) found trophic overlap was slightly greater in winter than summer for co-existing *N. fodiens* and *S. coronatus* but remained the same for *N. fodiens* and *Galemys pyrenaicus*. Foraging modes and niche overlap in overwintering shrews in northern temperate habitats should be addressed in future studies.

Stomach analyses by Kuvikova (1985b) of *N. fodiens*, *N. anomalus*, *S. araneus* and *S. minutus* from alder forest in Slovakia showed that all species ate mainly terrestrial prey, also implying that very high overlap can be tolerated amongst these shrews. One explanation is that terrestrial food resources were in plentiful supply and terrestrial foraging is easier and energetically less costly than aquatic foraging. Where attempts have been made to quantify food supply, they have confirmed that shrews are generalist, opportunist predators that feed on common and abundant invertebrates with relatively little selection for prey type (Churchfield, 1982, 1984a; Churchfield *et al*., 1991; DuPasquier & Cantoni, 1992; Castién & Gosálbez, 1999). This is supported by our study, although some selection for certain prey taxa is indicated. Inevitably this will lead to overlap between species. Morphological and size differences between shrews equip them for slightly different foraging modes that help to reduce overlap and permit coexistence.

Acknowledgements

We are very grateful to A. Arasim, J. Hejduk, E. Jancewicz, T. Kłosińska and M. Ściński for field and technical assistance. This study was supported by the Polish Ministry of Scientific Research and Information Technology (research grant No. 6 P04F 036 21) and Centre of Excellence BIOTER (Contract No. EVK2-CT-2002-80011, European Commission's 5th Framework Programme).

REFERENCES

Aitchison, C.W. (1978). Spiders active under snow in southern Canada. *Symp. Zool. Soc. (Lond.)* **42**: 139-148.

Aitchison, C.W. (1979a). Notes on low temperature activity of oligochaetes, gastropods and centipedes in southern Canada. *Am. Midl. Nat.* **102**: 399-400.

Aitchison, C.W. (1979b). Winter-active subnivean invertebrates in southern Canada. II. Coleoptera. *Pedobiologia* **19**: 121-128.

Begon, M., Townsend, C.R. & Harper, J.L. (2005). *Ecology. From individuals to ecosystems*. 4th edition. Blackwell Publishing, Oxford, pp. 784.

Borowski, S. & Dehnel, A. (1952). [Data on biology of Soricidae]. *Annals Univ. M. Curie-Skłod.* (C) **7**: 305-448. [In Polish with Russian and German summaries]

Castién, E. (1995). The diet of *Neomys fodiens* in the Spanish Western Pyrenees. *Folia Zool.* **44**: 297-303.

Castién, E. & Gosálbez, J. (1999). Habitat and food preferences in a guild of insectivorous mammals in the Western Pyrenees. *Acta Theriol.* **44**: 1-13.

Churchfield, S. (1980). Population dynamics and the seasonal fluctuations in numbers of the common shrew in Britain. *Acta Theriol.* **25**: 415-424.

Churchfield, S. (1982). Food availability and the diet of the common shrew, *Sorex araneus*, in Britain. *J. Anim. Ecol.* **51**: 15-28.

Churchfield, S. (1984a). Dietary separation in three species of shrew inhabiting water-cress beds. *J. Zool. (Lond.)* **204**: 211-228.

Churchfield, S. (1984b). An investigation of the population ecology of syntopic shrews inhabiting water-cress beds. *J. Zool. (Lond.)* **204**: 229-240.

Churchfield, S. (1990). *The Natural History of Shrews*. Christopher Helm/A & C Black, London, pp. 178.

Churchfield, S. (1998). Habitat use by water shrews, the smallest of amphibious mammals. *Symp. Zool. Soc. (Lond.)* **71**: 49-68.

Churchfield, S. (2002). Why are shrews so small? The costs and benefits of small size in northern temperate *Sorex* species in the context of foraging habits and prey supply. *Acta Theriol.* **47**, Suppl. 1: 169-184.

Churchfield, S., Hollier, J. & Brown, V.K. (1991). The effects of small mammal predators on grassland invertebrates, investigated by field exclosure experiment. *Oikos* **60**: 283-290.

Churchfield, S., Nesterenko, V.A. & Shvarts, E.A. (1999). Food niche overlap and ecological separation amongst six species of coexisting forest shrews (Insectivora: Soricidae) in the Russian Far East. *J. Zool. (Lond.)* **248**: 349-359.

Churchfield, S. & Sheftel, B.I. (1994). Food niche overlap and ecological separation in a multi-species community of shrews in the Siberian taiga. *J. Zool. (Lond.)* **234**: 105-124.

Churchfield, S., Sheftel, B.I., Moraleva, N.V. & Shvarts, E. A. (1997). Habitat occurrence and prey distribution of a multi-species community of shrews in the Siberian taiga. *J. Zool. (Lond.)* **241**: 55-71.

Connell, J.H. (1983). On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* **122**: 661-696.

Croin Michielsen, N. (1966). Intraspecific and interspecific competition in the shrews *Sorex araneus* L. and *S. minutus* L. *Archs néerl. Zool.* **17**: 73-174.

Dehnel, A. (1950). [Studies on the genus *Neomys* Kaup]. *Annals Univ. M. Curie-Skłod.* (C) **5**: 1-63. [In Polish with Russian and English summaries]

Dickman, C.R. (1988). Body size, prey size, and community structure in insectivorous mammals. *Ecology* **69**: 569-580.

Dickman, C.R. & Huang, C. (1988). The reliability of faecal analysis as a method for determining the diet of insectivorous mammals. *J. Mammal.* **69**: 108-113.

DuPasquier, A. & Cantoni, D. (1992). Shifts in benthic macroinvertebrate community and food habits of the water shrew, *Neomys fodiens* (Soricidae, Insectivora). *Acta Oecol.* **13**: 81-99.

Ebensperger, L. A. & Bottomahan, C. (1997). Use of habitat, size of prey, and food-niche relationships of two sympatric otters in southernmost Chile. *J. Mammal.* **78**: 222-227.

Fisher, D.O. & Dickman, C.R. (1993). Body size-prey size relationships in insectivorous marsupial: tests of three hypotheses. *Ecology* **74**: 1871-1883.

Fowler, J. & Cohen, L. (1995). *Practical Statistics for Field Biology*. John Wiley & Sons, New York, pp. 227.

Grainger, J.P. & Fairley, J.S. (1978). Studies on the biology of the pygmy shrew, *Sorex minutus*, in the West of Ireland. *J. Zool. (Lond)* **186**: 109-141.

Hutterer, R. (1985). Anatomical adaptations of shrews. *Mammal Rev.* **15**: 43-55.

Hutterer, R. & Hürter, T. (1981). Adaptive Haarstrukturen bei Wasserspitzmausen (Insectivora, Soricinae). *Z. Säugetierk.* **46**: 1-11.

Illing, K., Illing, R. & Kraft, R. (1981). Freilandbeobachtungen zur Lebensweise und zum Revierberhalten der Europäischen Wasserspitzmaus, *Neomys fodiens* (Pennant, 1771). *Zool. Beitr.* **27**: 109-122.

Ivanter, E.V. (1994). The structure and adaptive peculiarities if pelage in soricine shrews. In *Advances in the biology of shrews* Merritt, J.F., Kirkland, G.L. & Rose, R.K. (Eds). *Spec. Publs. Carnegie Mus. Nat.* Hist. 18: 441-454.

Kraft, R. & Pleyer, G. (1978). Zur Ernährungsbiologie der Europäischen Wasserspitzmaus, *Neomys fodiens* (Pennant, 1771), an Fischteichen. *Z. Säugetierk.* **43**: 321-330.

Kuvikova, A. (1985a). Zur Nahrung der Wasserspitzmaus, *Neomys fodiens,* in der Slowakei. *Biológia* (Bratislava) **40**: 563-572.

Kuvikova, A. (1985b). The food of some species of the family Soricidae (Insectivora) in the alder forest of the Jursky sur wetland. *Biológia* (Bratislava) **40**: 181-187. [In Slovak with English abstract].

Kuvikova, A. (1987). Zur Nahrung der Sumpfspitzmaus *Neomys anomalus* Cabrera, 1907 (Insectivora, Soricidae) in der Slowakei. *Lynx* (Praha) **23**: 55-62.

Lodé, T. (1993). Diet composition and habitat use of sympatric polecat and American mink in western France. *Acta Theriol.* **38**: 161-166.

Mezherin, V.A. (1960). Population density of *Sorex araneus* and its changes over 17 years. *Zool. Zhurn.* **39**: 1080-1087. [In Russian with English summary]

Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Kryštufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J.B.M., Vohralík, V. & Zima, J. (1999). *The Atlas of European Mammals.* Poyser Natural History. T. & A.D. Poyser/ Academic Press, London, pp. 484.

Näsmark, O. (1964). Subniveal winter activity in terrestrial invertebrates. *Zool. Revy* **26**: 5-15. [In Swedish with English summary].

Niethammer, J. (1977). Ein syntopes Vorkommen der Wasserspitzmäuse *Neomys fodiens* und *Neomys anomalus*. *Z. Säugetierk.* **42**: 1-6.

Niethammer, J. (1978). Weitere Beobachtungen über Wasserspitzmäuse der Arten *Neomys fodiens* und *N. anomalus*. *Z. Säugetierk.* **43**: 313-321.

Oksanen, L., Fretwell, S.D., and Järvinen, O. (1979). Interspecific aggression and the limiting similarity of close competitors: the problem of size gaps in some community arrays. *Am. Nat*. **114**: 117-129.

Pianka, E.R. (1973). The structure of lizard communities. *Ann. Rev. Ecol. Syst.* **4**: 53-74.

Pernetta, J.C. (1976). Diets of the shrews *Sorex araneus* L. and *Sorex minutus* L. in Wytham grassland. *J. Anim. Ecol.* **455**: 899-912.

Ramalhinho, M. G. (1995). Preliminary account of the biology of *Neomys anomalus* Cabrera, 1907 in Portugal. In *Proceedings of the seminar on the biology and conservation of European desmans and water shrews* (*Galemys pyrenaicus*, *Desmana moschata*, *Neomys* spp.), Ordesa, Spain, 7-11 June 1995. Council of Europe, Strasbourg, T-PVS (95) 32: 63-66.

Rudge, M.R. (1968). Food of the common shrew, *Sorex araneus*, in Britain. *J. Anim. Ecol.* **37**: 565-581.

Rychlik, L. (1997). Differences in foraging behaviour between water shrews: *Neomys anomalus* and *Neomys fodiens*. *Acta Theriol.* **42**: 351-386.

Rychlik, L. (2000). Habitat preferences of four sympatric species of shrews. *Acta Theriol.* **45**: 173-190.

Rychlik, L. (2005). Overlap of temporal niches among four sympatric species of shrews. Acta Theriol. **50**: 175–188.

Rychlik, L. & Jancewicz, E. (2002). Prey size, prey nutrition, and food handling by shrews of different body sizes. *Behav. Ecol.* **13**: 216-223.

Schoener, T.W. (1983). Field experiments on interspecific competition. *Am. Nat.* **122**: 240-285.

Somers, M. J. & Purves, M. G. (1996). Trophic overlap between three syntopic semi-aquatic carnivores: Cape clawless otter, spotted-necked otter and water mongoose. *Afr. J. Ecol.* **34**: 158-166.

Spitzenberger, F. (1990). *Neomys fodiens* (Pennant, 1771) - Wasserspitzmaus. In *Handbuch der Säugetiere Europas*. *Band 3, 1. Insektenfresser-Herrentiere*. Niethammer, J. & Krapp, F. (Eds). Aula-Verlag, Weisbaden: 334-374.

Voesenek, L.A.C.J. & Van Bemmel, A.C. (1984). Intra- and interspecific competition in the water shrew in the Netherlands. *Acta Theriol.* **29**: 297-301.

Vogel, P., Bodmer, C., Spreng, M. & Aeschimann, J. (1998). Diving capacity and foraging behaviour of the water shrew (*Neomys fodiens*). *Symp. Zool. Soc. (Lond.)* **71**: 31-47.

Wołk, K. (1976). The winter food of the European water-shrew. *Acta Theriol.* **21**: 117-129.

Zalewski, A. (2004). Geographical and seasonal variation in food habits and prey size of the European pine martens. In *Martens and fishers (Martes) in human-altered environments: an international perspective.* Harrison, D.J., Fuller, A.K. & Proulx, G. (Eds). Springer, New York, pp: 77-98.

Table 1. Frequency of occurrence (%) of invertebrate prey in the summer diets of four shrews species co-existing in marshland in Bialowieza Forest, eastern Poland.

Prey type	*N. fodiens*	*N. anomalus*	*S. araneus*	*S. minutus*
n=	30	13	30	13
TERRESTRIAL				
Coleoptera: Carabidae	22,6	30,8	6,3	7,7
Coleoptera: Staphylinidae	6,5	7,7	6,3	15,4
Coleoptera: Chrysomelidae	3,2	7,7	0,0	0,0
Other Coleoptera adults indet.	32,3	38,5	56,3	46,2
Coleoptera larvae	6,5	23,1	31,3	30,8
Formicidae	12,9	0,0	25,0	15,4
Diptera adults	22,6	46,2	21,9	38,5
Diptera larvae: Tipulidae	3,2	0,0	0,0	7,7
Diptera larvae: Bibionidae	0,0	0,0	6,3	0,0
Diptera larvae: Fannidae	0,0	0,0	0,0	7,7
Diptera larvae indet.	29,0	23,1	28,1	7,7
Lepidoptera adults	0,0	0,0	3,1	0,0
Lepidoptera larvae	6,5	30,8	21,9	7,7
Heteroptera	3,2	15,4	25,0	30,8
Collembola	3,2	0,0	3,1	15,4
Other insects indet.	0,0	7,7	6,3	0,0
Lithobiomorpha	0,0	0,0	3,1	0,0
Diplopoda: Juliformia	61,3	38,5	3,1	0,0
Isopoda	0,0	7,7	9,4	7,7
Araneae	74,2	76,9	63,3	92,3
Opiliones	29,0	53,8	16,6	69,2
Acarina	6,5	46,2	6,3	15,4
Mollusca	12,9	23,1	31,3	7,7
Lumbricidae	45,2	100,0	90,6	23,1
TERRESTRIAL/AQUATIC?				
Mollusca	22,6	46,2		
AQUATIC				
Trichoptera larvae	12,9	15,4		
Ephemeroptera nymphs	3,2	0,0		
Heteroptera: Gerridae	6,5	7,7		
Coleoptera adults indet.	12,9	0,0		
Coleoptera larvae indet.	0,0	7,7		
Diptera larvae: Ptychopteridae	9,7	0,0		
Diptera larvae: Stratiomyidae	6,5	15,4		
Diptera larvae: Tabanidae	6,5	15,4		
Asellus	51,6	23,1		
Diversity index (*H'*)	2,74	2,66	2,50	2,60

Table 2. Dietary overlap between four shrew species inhabiting marshland in Bialowieza Forest, eastern Poland.

Species compared	Shared prey (Sorensen QS)	Dietary composition (O_{ab})	Prey size (O_{ab})
N. fodiens & *N. anomalus*	81,6	83,8	95,2
N. fodiens & *S. araneus*	68,1	66,8	93,1
N. fodiens & *S. minutus*	72,7	44,4	77,6
N. anomalus & *S. araneus*	72,7	87,7	94,1
N. anomalus & *S. minutus*	68,3	62,7	90,3
S. araneus & *S. minutus*	82,1	67,1	76,6

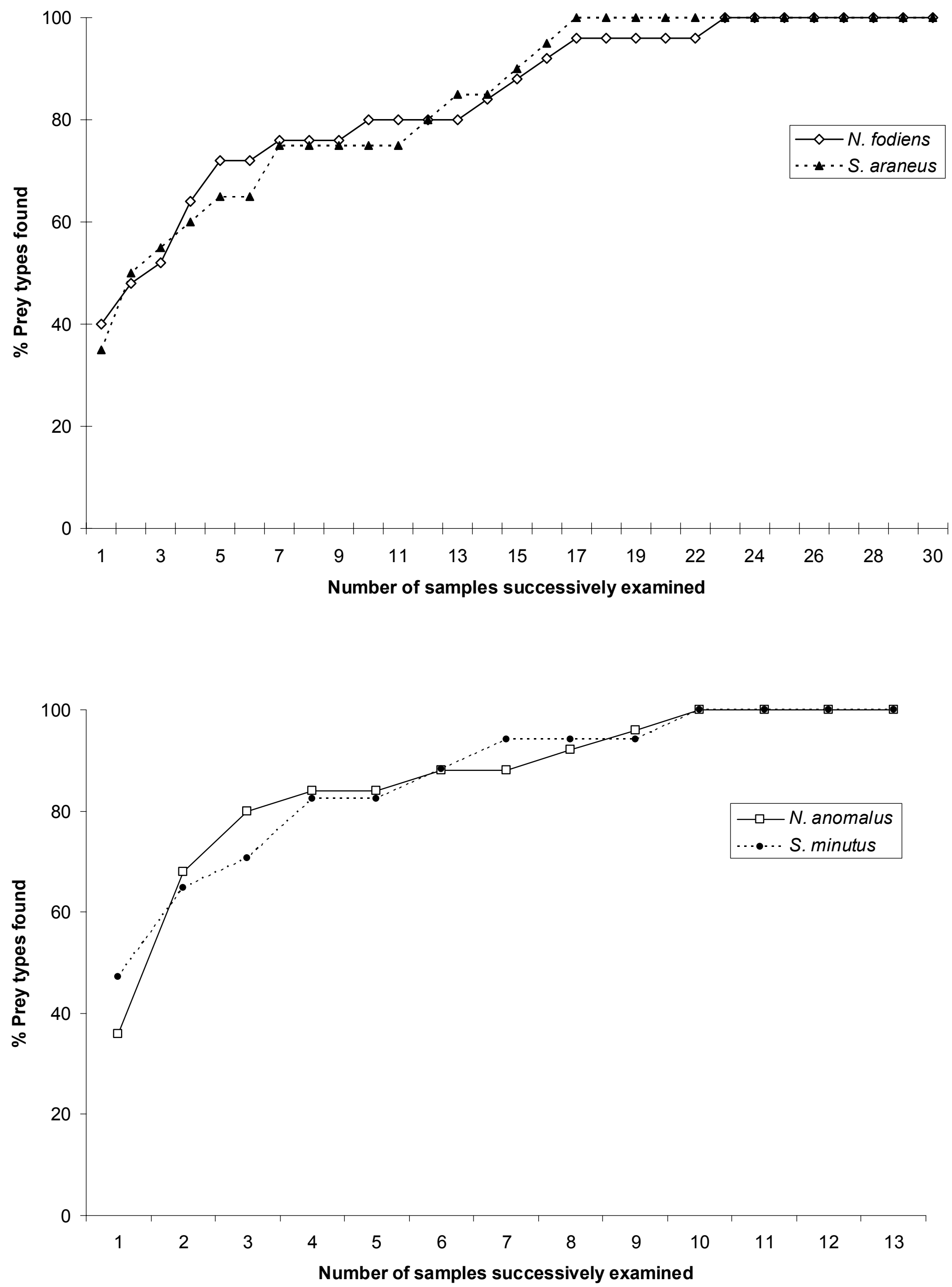

Fig. 1. Cumulative number of prey types found as successive faecal samples were examined.

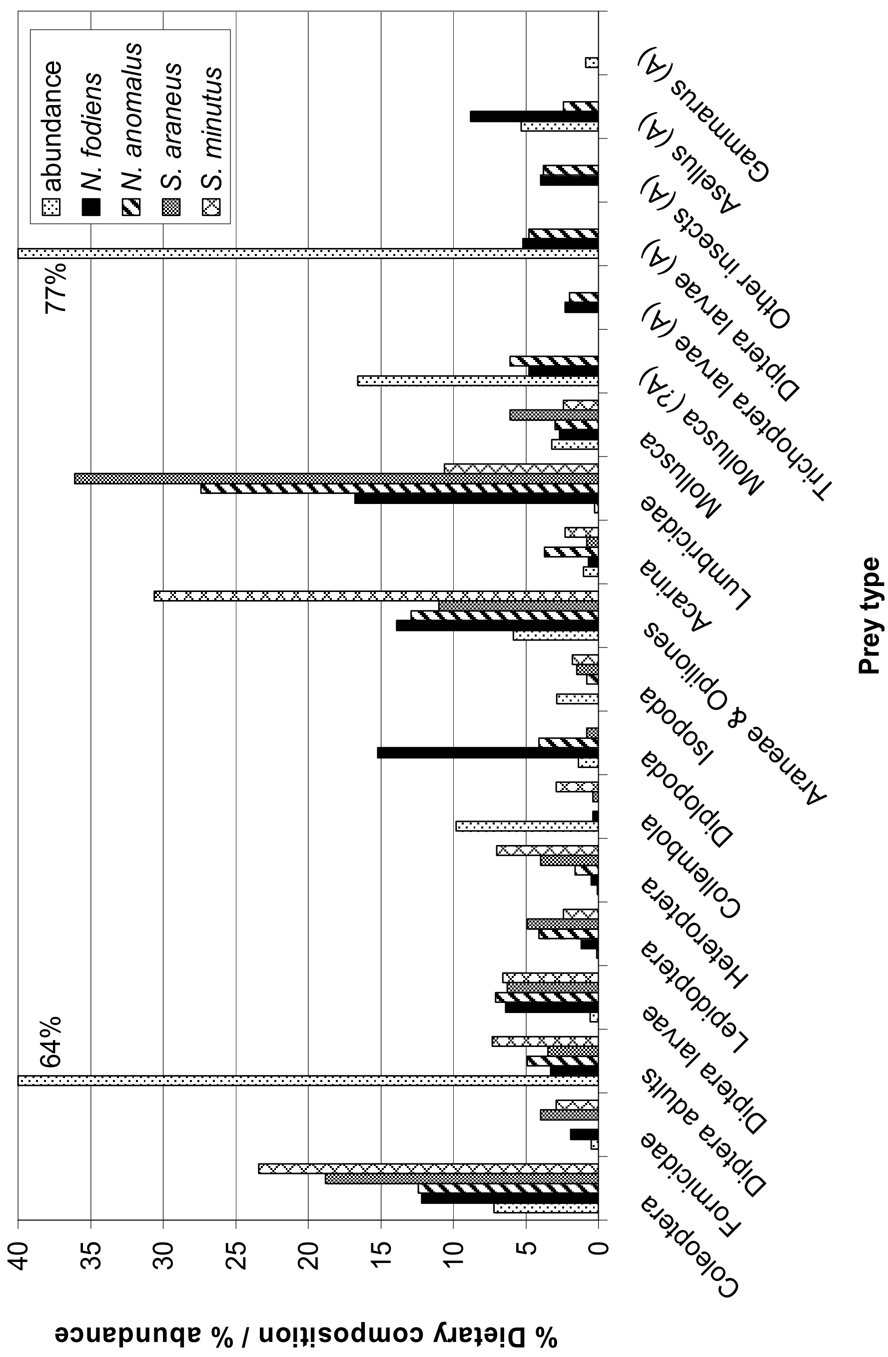

Fig. 2. The percentage composition of invertebrates in the summer diets of *Neomys* and *Sorex* shrews inhabiting marshland in Białowieża Forest, eastern Poland, together with the relative abundance of terrestrial and aquatic invertebrates in field samples. Aquatic items are marked (A).

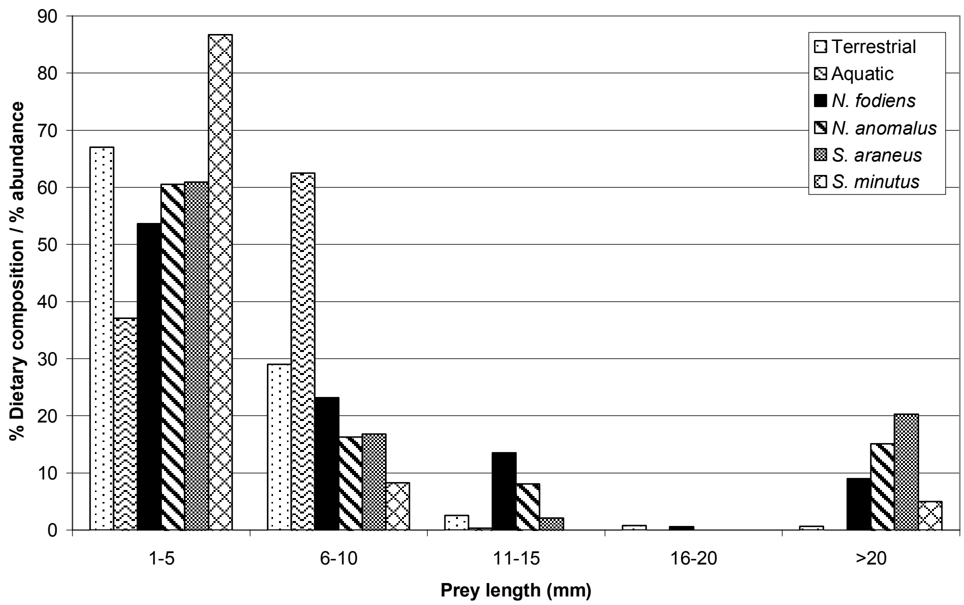

Fig. 3. The percentage dietary composition of prey in different size classes eaten by the four shrew species inhabiting marshland in Białowieża Forest, eastern Poland, together with the relative abundance of terrestrial and aquatic invertebrates in field samples.

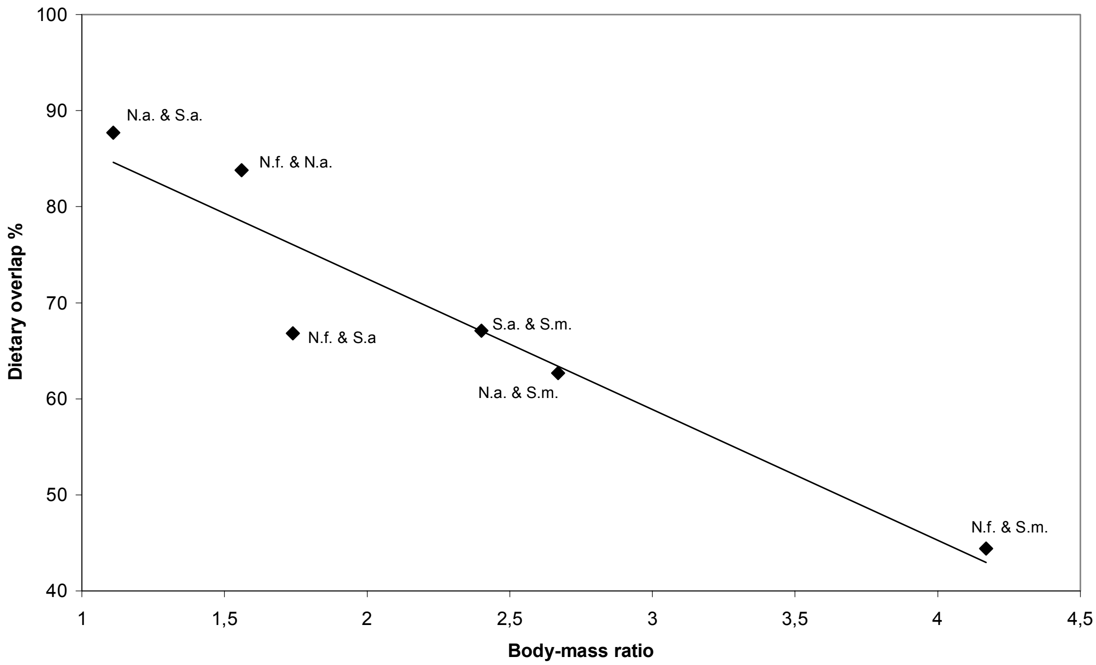

Fig. 4. Food niche overlap (dietary composition) between species-pairs of shrews plotted against their body-mass ratios (r_s= -0.947, p< 0.01). N.f.= *N. fodiens*, N.a.= *N. anomalus*, S.a.= *S. araneus*, S.m.= *S. minutus*.