Prey size, prey nutrition, and food handling by shrews of different body sizes

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We tested some predictions relating metabolic constraints of foraging behavior and prey selection by comparing food handling and utilization in four sympatric shrew species: *Sorex minutus* (mean body mass = 3.0 g), *S. araneus* (8.0 g), *Neomys anomalus* (10.0 g), and *N. fodiens* (14.4 g). Live fly larvae, mealworm larvae, and aquatic arthropods were offered to shrews as small prey (body mass <0.1 g). Live earthworms, snails, and small fish were offered as large prey (>0.3 g). The larvae were the highnutrition food (>8 kJ/g), and the other prey were the low-nutrition food (<4 kJ/g). The smallest shrew, *S. minutus*, utilized (ate + hoarded) <30% of offered food, and the other species utilized >48% of food. The larger the shrew, the more prey it ate per capita. However, highly energetic insect larvae composed 75% of food utilized by *S. minutus* and only >40% of the food utilized by the other species. Thus, inverse relationships appeared between shrew body mass and mass-specific food mass utilization and between shrew body mass and mass-specific food energy utilization: the largest shrew, *N. fodiens*, utilized the least food mass and the least energy quantity per 1 g of its body mass. Also, the proportion of food hoarded by shrews decreased with increase in size of shrew. With the exception of *S. araneus*, the size of prey hoarded by the shrews was significantly larger than the size of prey eaten. Tiny *S. minutus* hoarded and ate smaller prey items than the other shrews, and large *N. fodiens* hoarded larger prey than the other shrews. *Key words:* energy requirements, food hoarding, foraging behavior, optimal foraging strategy, prey energetic value, prey size preferences. [*Behav Ecol* 13:216–223 (2002)]

A lmost all soricine shrews have extremely high metabolic rates and food requirements (Genoud, 1988; Taylor, 1998; Vogel, 1980). Thus, the common opinion that they eat all prey which they are able to overpower is correct to some degree. However, there are at least ninefold differences in body size among soricine shrews: from 2.0 g in *Sorex minutissimus* to 18.1 g in *Blarina brevicauda* (male masses; Innes, 1994). This variation must lead to interspecific differences in metabolism as well as differences in prey preferences and foraging behavior (Hanski, 1985, 1994).

Total basic metabolic rates (BMRs) increase with shrew body size (Genoud, 1988; Hanski, 1984; Taylor, 1998; Vogel, 1980). Hence, total energy and food requirements should be higher in large shrews than in small shrews. In contrast, massspecific metabolic rates decrease with increasing shrew body size (Hanski, 1984, 1994; Taylor, 1998). This means that energy requirements and food consumption per unit of body mass should be higher in small than in large shrew species.

Besides higher mass-specific metabolic rates, small shrews also have smaller body energy reserves (Hanski, 1994), and they are therefore more sensitive to food shortages (Hanski, 1985). The function of body energy reserves may be replaced by food hoarding (Hanski, 1994; McNamara et al., 1990; Saarikko, 1989). Hence short-term food hoarding should be more important and common in small shrews than in large shrews (Hanski, 1989, 1994; Lucas and Walter, 1991; McNamara et al., 1990; Saarikko, 1989). Small shrews have less ability to defend food resources, and they should display a stronger tendency to scatter hoard than large shrews (Jenkins and Breck, 1998; Vander Wall, 1990).

To a foraging animal, each food item has two components: its present value for immediate consumption and its future value if stored. The future value is positively correlated with energy and nutrient content and with probability of consuming the food item in the future (Kotler et al., 1999). According to the theory (Andersson and Krebs, 1978), animals should hoard only food with a small C/G-ratio (where C is the fitness cost of hoarding one item, and G is the fitness gain from eating one stored item). The fitness gain includes both energy and survival; thus this condition holds true for the two foraging strategies: harvest rate maximization and survival rate maximization (Lucas and Walter, 1991). Shrews can adopt both strategies. There are several reasons that large prey should be more suitable for hoarding than small prey (Rychlik, 1999a): (1) transporting several large prey to the shelter is probably energetically less costly than transporting many small ones; (2) few transports of large prey expose the shrew to predation less than do multiple transports of small prey; (3) the frequency of interactions with competitors is decreased; (4) big prey have a better volume-to-surface ratio, so they may decay or dry up (or freeze in winter) and harden more slowly than the small ones. Thus, hoarding of relatively large prey can be expected in shrews.

There is little experimental evidence to support the above predictions, and comparative studies of food caching in small and large species are needed (Hanski, 1994). It has been proved that the most profitable prey (in the sense of the net energy gain per unit of handling time) for both small and large shrews are relatively large prey (Dickman, 1988; Hanski, 1992). In fact, shrews usually preferred (took and ate) large over small prey in laboratory experiments (Barnard and Brown, 1981; Barnard and Hurst, 1987; Dickman, 1988; Rychlik, 1997, 1999a; Vogel et al., 1998). According to Barnard and Brown (1981), shrews choose prey on the basis of size rather then energetic profitability. However, many theoretical and empirical studies (Fryxell and Lundberg, 1994; Pierce et al., 1993; Sih and Christensen, 2001; and references cited

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Table 1

Mean (± 1 SE, n = 10) body masses of shrews tested in the present study and mass-specific basic metabolic rates (BMR) of the four species under study (averages from values given for each species by Taylor, 1998)

Species	Body mass (g)	$\frac{\text{BMR}}{(\text{ml }O_2/\text{g}\times\text{h})}$
Sorex minutus	3.0 ± 0.13	9.62
Sorex araneus	8.0 ± 0.29	7.38
Neomys anomalus	10.0 ± 0.51	4.98
Neomys fodiens	14.4 ± 0.61	3.61

therein) showed that shrews and other animals violate the "zero-one selection rule" of optimal foraging theory and display partial preferences. A lack of prey-size preferences was also observed, for example, in "cafeteria tests" with 3-, 10-, and 25-mm pieces of mealworm larvae offered to *Sorex minutus* and *S. araneus* (Churchfield, 1991).

Studies of shrews' natural diets showed that most shrews (including the large species) ate many tiny (< 5 mm long) prey, and even very small shrews take some large (> 30 mm) prey (Churchfield, 1991, 1994; Churchfield and Sheftel, 1994). On the other hand, large shrews display some specialization and preference to hunt on large prey, and small shrews show specialization and preference for small prey in the wild (Churchfield, 1991; Churchfield and Sheftel, 1994; Dickman, 1988). Thus, these problems need further investigation.

Although energy is the most popular currency for use in optimal foraging models, many studies have concentrated on relationships between prey size or taxon and predator search time, handling time, and capture efficiency, and only few studies have assessed prey energy values (Brooks et al., 1996). As was the case 17 years ago (Hanski, 1984), there are still too few investigations concerning the natural food requirements of shrews (most previous studies were done with artificial diets). Unfortunately, artificial diets (as immobile pieces of mealworms or frozen fly pupae) were also used in most of the studies of food handling behavior and prey-size preferences, including the classical papers (e.g., Barnard and Brown, 1981; Krebs et al., 1977; Rechten et al., 1983). Meanwhile, prey mobility has been found to be crucial in foraging decisions (Sih and Christensen, 2001).

Many studies of prey-size preferences in shrews and insectivorous marsupials lasted only up to 15 min (see Rychlik, 1999a). Too short a period of observation may produce a false or incomplete picture of animal behavior. On the other hand, foragers change their foraging tactic from rate (net energy gain per unit time) maximization with high workload when time is limiting to efficiency (net energy gain per unit energy expenditure) maximization with low workload when foraging time is not limited (Ydenberg and Hurd, 1998). Longer experiments are therefore needed.

In the present study we compared food handling and utilization in four coexisting shrew species [*Sorex minutus* Linnaeus, 1766; *S. araneus* Linnaeus, 1758; *Neomys anomalus* Cabrera, 1907; and *N. fodiens* (Pennant, 1771)] of different body masses and BMRs (Table 1). Six live and active prey types of different size, energy content, and nutritional quality were used in cafeteria tests, and shrews were allowed to forage for 4 h. Because two shrew species were semiaquatic, two of six prey types were aquatic.

We tested the following predictions in this study: (1) massspecific food and energy consumption will decrease with the increase in body size of tested shrews, (2) food hoarding will decrease with an increase in shrew body size, (3) in all shrew species, prey hoarded will be larger than prey eaten, and (4) large shrews will utilize larger prey than small shrews.

MATERIALS AND METHODS

Trapping and keeping shrews in captivity

Wild shrews were trapped in the Białowieża Forest (eastern Poland) in summer (July and August). The trapping plot was located in a sedge swamp and crossed by a stream. Immediately after trapping, the animals were transported to a laboratory where they were kept individually in plastic cages ($30 \times 40 \times 15$ cm) covered with dense wire net. The substratum, composed of sand, sawdust, peat, and grass, was wetted daily. This bedding was changed every 3 weeks. One nest-box (reversed flower pot filled with moss) was placed in each cage. Non-test food (minced beef) and water were given ad libitum. There was the natural light-dark cycle in the laboratory, the temperatures were $16-20^{\circ}$ C, and the air humidity about 80%. Shrews underwent at least a 2-week-acclimatization to these conditions. During this period they could become familiar with test food (see below), which was given in small amounts.

Experimental procedure

"Cafeteria tests" (Pinowski and Drożdż, 1968) were carried out under the same humidity and temperature as keeping conditions. Shrews were tested individually in plastic cages (30 \times 40 \times 15 cm) with a nest-box (filled with cuttings of woodwool), a sheet of white paper on the floor, and six glass trays with test food. The cage was covered with a glass pane and illuminated with a 60-W lamp hung at the distance of 1.5 m. Tests were carried out during the daytime (mostly between 1000 and 1800 h), during the period of decreased feeding and locomotor activity of shrews (Buchalczyk, 1972). Tested shrews were fed with the non-test food at least 5 h before the experiment. Just before the test, some remaining non-test food was usually observed in the shrews' cages (besides the food hoarded by shrews in their nest-boxes). Thus, we assumed that shrews could feel some hunger but were not starved at the beginning of tests.

We used six live prey types as the test food: fly (*Calliphora* sp.) larvae, mealworm (*Tenebrio molitor*) larvae, earthworms (*Lumbricus* sp.), snails (*Succinea* sp.), aquatic arthropods (mostly of genera *Asellus* and *Gammarus*, and a few aquatic insect larvae), and small fish (sticklebacks *Gasterosteus aculeatus* and fry of roach *Rutilus rutilus*). Aquatic arthropods and fish were the aquatic prey (given in water about 3 cm deep), the remaining types were terrestrial prey. Earthworms, snails, and fish were small prey (Table 2). Small prey were about four times lighter than large prey (Mann-Whitney test: U = 0.0-1673.5, p < .001), and twice as many small prey were given than large prey (U = 0.0-4920.0, p < .001).

Only the exact handling times for mealworms $(23-28 \text{ mm} \log, 122.5 \pm 13.0 \text{ mg} \text{ of wet mass})$ were known: $23.7 \pm 5.9 \text{ s}$ for *N. fodiens*, $30.2 \pm 5.5 \text{ s}$ for *N. anomalus*, $33.4 \pm 6.5 \text{ s}$ for *S. araneus*, and $57.6 \pm 13.1 \text{ s}$ for *S. minutus* (Haberl, 1998). Handling times for the other prey were not measured or known from the literature. However, according to their body length, hardness, escape abilities, and so on, the prey can be ordered with an ascending handling time: (1) fly larvae (short, the softest), (2) mealworm larvae (medium length, soft), (3) aquatic arthropods (short and soft but under water), (4) earthworms (the longest, resilient), (5) snails (medium, in hard shells), and (6) fish (medium, with bones and scales, quickly moving under water).

The following energetic values of the prey were accepted

Prey type	No. of items	Mass of all items	Mass of one item	
Fly larvae (L)	$9.98 \pm 0.01 \text{ E,S,F}^{a}$	0.86 ± 0.01 E,S,A,F	$0.09 \pm 0.00 \text{ E,S,F}$	
Mealworm larvae (M)	$10.00 \pm 0.00 \text{ E,S,F}$	$0.86 \pm 0.03 \text{ E,S,A,F}$	$0.09 \pm 0.00 \text{ E,S,F}$	
Earthworms (E)	$4.11 \pm 0.09 \text{ L,M,S,A,F}$	$1.52 \pm 0.05 \text{ L,M,S,A,F}$	0.38 ± 0.01 L,M,A,F	
Snails ^b (S)	5.00 ± 0.00 L,M,E,A,F	$1.91 \pm 0.10 \text{ L,M,E,A,F}$	0.38 ± 0.02 L,M,A	
Aquatic arthropods (A)	$9.79 \pm 0.47 \text{ E,S,F}$	0.48 ± 0.02 L,M,E,S,F	$0.08 \pm 0.01 \text{ E,S,F}$	
Fish (F)	3.70 ± 0.09 L,M,E,S,A	1.08 ± 0.05 L,M,E,S,A	0.32 ± 0.02 L,M,E,A	
Total	42.58 ± 0.41	6.71 ± 0.17	0.16 ± 0.00	

Table 2

	Mean (± 1	SE)	numbers and	masses ((g)	of	prey	offered	to	shrews	per o	one	cafeteria	test	(n =	120	tests)
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^a Within columns, significant differences (Mann-Whitney test: p < .05) between values obtained for particular prey types are indicated by letters. For example, the number of items of fly larvae (L) differed significantly from those of earthworms (E), snails (S) and fish (F). ^b Mass of shells included.

from literature: 8.4 kJ/g of wet body mass for fly larvae (Hawkins and Jewell, 1962), 10.5 kJ/g for mealworm larvae, 2.9 kJ/ g for earthworms, and 2.9 kJ/g for snails (Ruthardt, 1990), 3.7 kJ/g for aquatic arthropods [an average of the value for *Asellus aquaticus* (3.2 kJ/g; Prus, 1977) and for *Gammarus* spp. (4.2 kJ/g; Ruthardt, 1990)], and 3.0 kJ/g for small fish (Fischer, 1970). Prey were given on open trays placed next to each other (trays covered an area of $< 200 \text{ cm}^2$) and at a distance up to 15 cm from the next box.

Test food was prepared 30 min before a test. The number of items and total mass of each prey type were recorded. The tested shrew was weighed just before the experiment. The weighing accuracy was 0.1 g for shrews and 0.01 g for prey. Next, we placed the shrew in the test cage and left it undisturbed for 5 min. During this time shrews usually explored the cage and hid in the nest-box. Six trays, each containing a test food type, were then randomly placed within the cage, and the shrew was allowed to forage for 4 h. Immediately after the 4-h period we removed the shrew from the cage.

In total, 40 juvenile or subadult shrews (10 of each species) were used in a random order. Each shrew was tested for 3 successive days (to reduce intraindividual variation) and 4 h per day. This resulted in 12 h of observations for each individual, 120 h for each species, and 480 h for all shrews.

Analysis of data

We calculated the average mass of one prey item of a given category for each test. Immediately after each test, the number and mass of prey of each type left by the shrew on trays, hoarded in the nest-box, and abandoned in the cage out of the trays and the nest-box (three categories of prey handling) were noted. We categorized partially eaten prey items as eaten in 1/5, 1/4, 1/3, 1/2, 2/3, 3/4, or 4/5. On the basis of this information, the number and mass of prey of each type eaten by the shrew (fourth category) was calculated. Prey left + abandoned was treated as nonutilized food, whereas prey hoarded + eaten was treated as utilized food.

Next, for each shrew and each analyzed parameter, we averaged the three values from 3 succeeding days and obtained first-degree averages (1°). These 1° averages were treated as sample trials. They were compared using Wilcoxon and Mann-Whitney tests and regression analysis (GraphPAD InStat 1.13, 1990; SYSTAT 5.01, 1992). In the figures, 2° averages, calculated from 1° averages, are shown.

RESULTS

All interspecific differences in the body mass of tested shrews were statistically significant (Mann-Whitney test: U = 0.0-11.0,

p < .005). The smallest *Sorex minutus* was nearly five times lighter than the largest *Neomys fodiens* (Table 1).

With regard to prey handling (Figure 1a), the pigmy *S. minutus* left the most food on trays; the proportion of this category was significantly higher than the proportions of abandoned, hoarded, and eaten categories (Wilcoxon test: W = 55, p = .002 for the all three comparisons). *S. minutus* also abandoned quite a lot of taken prey (20.9%). Thus, the proportion of nonutilized food (left + abandoned = 71.1%) was much higher than that of utilized food (hoarded + eaten = 28.9%; W = 55, p = .002).

The proportions of utilized and nonutilized food by *S. araneus* were nearly equal (48.5% vs. 51.5%; difference insignificant). These shrews also ate and left on trays similar quantities of prey (39.0% vs. 43.6%, difference insignificant; Figure 1a). The two *Neomys* species ate significantly more food than they hoarded, abandoned, and left on trays (W = 43-55, p = .002-.027). However, the proportions of nonutilized food were still quite high (37.3% in *N. anomalus* and 43.0% in *N. fodiens*), and they did not differ significantly from proportions of utilized food (Figure 1a).

Interspecific comparisons revealed that the two *Sorex* species left significantly more prey on trays than the two *Neomys* species (Mann-Whitney test: U = 5.0-18.0, p = .001-.018). *S. araneus* abandoned significantly less prey than the three other species (U = 11.0-19.5, p = .004-.024). The largest *N. fodiens* hoarded less food than the other species (significantly less than *N. anomalus* and *S. minutus*; U = 19.0 and 23.0, p < .05), but it ate more food than the other species (significantly more than *S. minutus*; U = 0.0, p < .001). *S. minutus* ate significantly less prey than the other species (U = 0.0-7.0, p < .002). *N. anomalus* and *S. araneus* hoarded and ate food in similar proportions. *S. minutus* utilized significantly less food than the three other species (U = 8.0-21.0, p = .002-.032; Figure 1a).

The analysis of prey utilization (hoarding vs. eating; Figure 1b) showed that all species ate proportionally more food than they hoarded. The smallest difference was for the tiny *S. minutus* (Wilcoxon test: W = 45, p = .02), whereas for the other species the differences were highly significant (W = 55, p = .002). There were not significant differences in prey utilization between *S. araneus* and *N. anomalus*, the two mediumsize species. But the large *N. fodiens* hoarded less food than the medium-sized species (significantly less than *N. anomalus*; U = 20.0, p = .026). In contrast, *S. minutus* hoarded proportionally more food than the medium-sized shrews (significantly more than *S. araneus*; U = 21.0, p = .032) and much more than *N. fodiens* (U = 9.0, p < .003).

The prey of high energetic value (larvae of mealworms and



Figure 1

(a) Prey handling and (b) utilization by the four shrew species of different body masses. Distinguished categories: eaten, proportion of prey items eaten by shrews; hoarded, prev hidden in the nest-box; abandoned, prev abandoned in the cage out of the nest-box, left on travs, prev not taken. 100% = (a) numbers of all items given at the beginning of particular test or (b) number of items eaten and hoarded during particular test. S.m., Sorex minutus; S.a., Sorex araneus; N.a., Neomys anomalus; N.f., Neomys fodiens.

fly) composed 80% of food eaten and 75% of food utilized by S. minutus (Figure 2). In contrast, these prey composed only > 48% of food eaten and 40% of food utilized by the three other species. S. araneus ate as much as 66% of low energetic prey (earthworms and snails; Figure 2a).

Total masses of prey eaten and utilized by shrews showed a high positive dependence on the body mass of shrews (Figure 3a,d). In contrast, masses of prey eaten and utilized per unit of shrews' body mass were negatively related to the size of shrews (Figure 3b,e). This relationship was significant for food utilization (Figure 3e). A high negative dependence on the shrews' body mass was found for the total energy of prey eaten and utilized by shrews (Figure 3c,f).

Mean total masses and energetic values of food eaten and utilized by shrews of particular species were also compared (Figures 2 and 3). Interspecific comparisons showed that medium-sized shrews, S. araneus and N. anomalus, ate similar masses of prey (Figures 2a and 3a). Large N. fodiens ate significantly more food than the three other species (Mann-Whitney test: U = 0.0-19.0, p = .001-.021), and tiny S. min*utus* ate significantly less food than all the other species (U =0.0–2.0, p < .001). The difference between the masses of food utilized by medium-sized S. araneus and N. anomalus was insignificant. S. minutus utilized significantly less food than the three other species (U = 2.0-7.5, p < .002), and N. fodiens utilized more food than the other species (but the difference was significant only between N. fodiens and S. minutus; U =2.0, p < .001; Figures 2b and 3d).

Smaller shrews, on average, ate and especially utilized more food per unit of body mass than larger shrews (Figure 3b,e). However, none of the interspecific differences in these parameters were significant. As to the mean total energy of food eaten and utilized by shrews (Figure 3c,f), the only significant differences were between S. *minutus* and the two Neomys species (U = 17.0, p = .014 for mass-specific energy consumption and U = 8.0 and 18.0, p < .002 and .018 for utilization). Nevertheless, a clear tendency of the inverse relationships between shrews' mean body mass and mean mass-specific consumption and utilization of energy was observed (Figure 3c,f).

Except S. araneus, all shrews hoarded significantly larger prey items than those which they ate (Wilcoxon test: W = 28-43, p = .016-.039; Figure 4). Pigmy S. minutus hoarded significantly smaller prey than the three other species (Mann-Whitney test: U = 0.0-17.0, p = .001-.02). This species also



Masses of particular prey types (a) eaten and (b) utilized by the four species of shrew. Species abbreviations as in Figure 1.



Figure 3

Relations between body mass of shrews and (a) total prey consumption, (b) mass-specific prey consumption, (c) mass-specific energy consumption, (d) total prey utilization, (e) mass-specific prey utilization, and (f) mass-specific energy utilization. Utilization means eating + hoarding of prey. Points marked by different symbols represent mean (from three successive tests) values obtained for individual shrews. Lines show the regressions based on these points. Bars show mean values (+ 1 SE) obtained for particular species. Circle: *S.m., Sorex minutus*; square: *S.a., Sorex araneus*; star: *N.a.: Neomys anomalus*; down triangle: *N.f., Neomys fodiens*.



Figure 4

Mean (+ 1 SE) masses of prey items hoarded and eaten by the four shrew species of different body masses. Intraspecific significant differences (Wilcoxon test: p < .05) between categories are indicated by asterisks.

ate smaller prey than the other shrews (significantly smaller than *S. araneus* and *N. fodiens*; U = 4.0 and 10.0, p < .001and .003, respectively). The large *N. fodiens* hoarded significantly larger prey than the other species (U = 0.0-5.5, p < .001-.005), but it ate prey of similar size as *N. anomalus* did, smaller than *S. araneus* (U = 17.0, p = .014), and larger only than *S. minutus* (U = 10.0, p < .003). The size of prey items hoarded by *S. araneus* and *N. anomalus* did not differ, but *S. araneus* ate significantly larger prey than the three other species (U = 4.0-17.0, p = .001-.014; Figure 4).

DISCUSSION

In other studies (Churchfield, 1982b; Hanski, 1984; Hawkins and Jewell, 1962), carried out under temperatures ranging from 11° to 23°C, *S. minutus, S. araneus*, and *N. fodiens* utilized from 1.2 to 1.7 g wet mass of prey per 4 h. We offered on average 6.7 g of prey per 4 h. As the result, our shrews ate maximum 53% of available prey (*N. fodiens*), and they left on trays at least 37% of food (*N. anomalus*). Therefore, the foraging behavior of our shrews was not affected by food scarcity (though it could be influenced by the overabundance of prey).

We believe that all our shrews had the same and simultaneous access to all prey types due to the food arrangement on trays and tray position. Thus, the interspecific differences found in prey handling and preferences could not result from different availability or difficulties in localization of particular prey types.

Per capita food consumption

As expected, per capita food consumption (as well as utilization) increased with an increase in shrew body mass. These results are not revelational, but so far there has not been clear and methodologically correct experimental evidence for this relationship in shrews. Hanski (1994) suggested that large shrews (body mass < 10 g) have approximately twice the food requirements of small species (< 5 g). In our study, the mass of food eaten by large *N. fodiens* was 4.6 times higher than in small *S. minutus*, and the medium-size *S. araneus* and *N. anomalus* ate 3.2 times more food than *S. minutus*. These differences are considerably higher than suggested by Hanski (1994). The disagreement between Hanski's estimation and our results may ensue from the different nutrient values of prey used in our experiment and his study, as well as from the relatively short duration of our tests.

It is interesting that the mean total masses of prey eaten by *S. araneus* and *N. anomalus* were the same (Figure 3a). This can be related to two mechanisms: (1) BMR is 1.48 times higher in *S. araneus* than in *N. anomalus* (Taylor, 1998), but our *S. araneus* were only 1.25 times lighter than *N. anomalus*. This may produce a relatively high food consumption in *S. araneus*. (2) Because of better insulation of fur, water shrews have lower thermal conductance than *Sorex* shrews (Taylor, 1998). This may additionally reduce the food requirements of *N. anomalus*.

Mass-specific food consumption

Generally, mass-specific consumption and utilization of food decreased with an increase in shrew body size. This was especially distinct for the consumption and utilization of energy. These results are consistent with our prediction. However, mass-specific consumption of food mass was unexpectedly low in *S. minutus*; it was lower than in *S. araneus* (Figure 3b). This can be explained by the fact that *S. minutus* reduced the total mass of consumed food by eating prey of better quality. It ate almost exclusively mealworm and fly larvae, which yield a lot of energy. Moreover, they contained little water and indigestible cuticle (Churchfield, 1993). In contrast, *S. araneus* ate, besides insect larvae, many earthworms and snails (Figure 2), which contain relatively little energy and a great deal of soil in their guts and water in their bodies (Churchfield, 1993).

Similarly, Hanski (1984) found that daily food consumption would be almost two times higher when shrews eat only beetles in comparison to a diet composed only of insect pupae. That was because utilization efficiency of ant pupae and sawfly cocoons (little cuticle) was clearly higher (70–85%) than that of beetles with thick chitin exoskeletons (45–60%). Our finding fits also with the general observation that larger shrew species usually eat prey of poorer quality than smaller shrews (Hanski, 1984; Okhotina, 1974; Yudin, 1962).

Food hoarding

Preparation of temporal scattered stores has been observed in many terrestrial and semiaquatic shrews (see Rychlik, 1999b), including the three species tested in our study (*S. araneus*: Churchfield, 1980; Crowcroft, 1955; Dehnel, 1961; *N. anomalus*: Rychlik, 1999a,b; *N. fodiens*: Hawkins and Jewell, 1962; Köhler, 1984; Rychlik, personal observation). Therefore, in our opinion, the hiding of food in the nest-box observed in the present study was an expression of the natural tendency of shrews to prepare temporal food hoards.

Theoretically, short-term food hoarding should be observed when (1) the metabolic costs of carrying reserves are high; (2) food supply is variable and unpredictable; (3) the mean rate of intake is low; (4) energy expenditure between foraging bouts is high; (5) remembering the location of caches is high or medium; (6) fat reserves are intermediate; (7) cache pilferage risk is low or medium; and (8) food perishability is low (Jenkins and Breck, 1998; Leaver and Daly, 1998; Lucas and Walter, 1991; McNamara et al., 1990). Moreover, short-term hoarding is usually "a suite of responses . . . both to environmental quality and current physiological state" (Lucas, 1994: 178). In shrews short-term hoarding has been found to be related to (1) presence of intra- and interspecific competitors in the vicinity (Barnard et al., 1983; Churchfield, 1990), (2) predation risk (Saarikko, 1989), (3) hunger level (Sorenson, 1962), (4) overabundance of prey (Buckner, 1964; Hamilton, 1930, 1944; Martin, 1984), (5) sex of shrews (Formanowicz et al., 1989), and (6) size and type of prey (Barnard and Brown, 1985; Formanowicz et al., 1989; Martin, 1984; Robinson and Brodie, 1982). Food hoarding observed in our study probably resulted from food overabundance and a low hunger level (intermediate fat reserves), and it was influenced by the size and type of prey (see below), which is in accordance with both theoretical and empirical data.

The proportion of food hoarded by shrews decreased with an increase in their size. The smallest *S. minutus* hid proportionally the greatest amounts of food, and the largest *N. fodiens* the least amounts. These results are consistent with our prediction. Short-term food hoarding should be especially important for small shrews because: (1) their ingestion capacity is low, (2) they cannot accumulate much energy in their body (in the form of adipose tissue), (3) they are more sensitive to food shortages than large shrews, and (4) they are not able to defend their food resources against larger competitors (Hanski, 1985, 1989, 1994; Jenkins and Breck, 1998; Lucas, 1994; Saarikko, 1989; Vander Wall, 1990).

It is surprising that we did not find reports on food hoarding in *S. minutus*, though this behavior was frequently observed in the other species under study (see above). Also, there are only a few and rather accidental observations (Formanowicz et al., 1989; Hamilton, 1944; Hanski, 1989) of food hoarding in other small shrews. Thus, our work gives the first clear evidence of the strong tendency to hoard food in the pigmy shrew *S. minutus*.

The interspectic differences in food hoarding may also be related to the differences in trophic specialization of particular shrews. It is clear that, in the wild, trophic specialists deal much more frequently with a scarcity of their particular food than trophic generalists do with their various food. Therefore, it is logical that trophic specialists have evolved a stronger tendency to hoard surplus food. S. minutus has been proved to be the trophic specialist, whereas S. araneus and especially N. fodiens are the trophic generalists (Castién and Gosálbez, 1999; Churchfield, 1991; Churchfield and Sheftel, 1994). Thus, our finding, that S. minutus hoarded proportionally the greatest amounts of food and N. fodiens the least amounts, supports this idea. The fact that N. anomalus hoarded proportionally more prey than S. araneus (rather an inverse tendency was expected according to their masses) can also be explained by the possibility that the level of trophic specialization is probably higher in N. anomalus than in S. araneus.

Size of hoarded versus eaten prey

As predicted, prey hoarded by all shrew species (except for *S. araneus*) were significantly larger than prey eaten. This is consistent with observations of different animals that display a tendency to eat small food items at once and hoard large ones (see Rychlik, 1999a).

The four reasons that large prey should be more suitable for hoarding than small prey were listed in the Introduction. Because our shrews were alone in the cage during tests, their foraging was not influenced by predators and competitors. Therefore, the tendency to hoard large prey observed in our study can be related to two mechanisms: (1) transportation of big prey to the shelter was probably energetically more profitable than transportation of small prey, and (2) big prey were probably more resistant to decaying than the small ones. However, the tendency toward hoarding large prey may partly result from the possibility that some hoarded prey were left in nest-boxes because they required too long a time to be eaten. For example, long and resilient earthworms (hoarded by all shrews except N. fodiens; Figure 2) could require a high dexterity in prey handling. Snails (hoarded in a high proportion by N. anomalus) could require a high bite force because of hard shells. Fish (hoarded in a high proportion by both water shrew species) could be difficult to digest because of bones. Differences in nutritional value and palatability could also contribute to the obtained results. Small prey are more suitable for eating than large prey because they are easier to manipulate and bite, which shortens the handling time per item.

These explanations are supported, for example, by the following findings: (1) Blarina brevicauda chose to eat small slugs and annelids and avoided the large ones (Hamilton, 1930); (2) these shrews ate soft mouse flesh and insects (easier to manipulate) before they ate hard sunflower seeds (Martin, 1984); (3) utilizing its food hoards, N. anomalus ate proportionally more small than big food portions (Rychlik, 1999a). In this context, our result obtained for S. minutus is especially interesting. These shrews hoarded and ate almost only small prey (i.e., fly and mealworm larvae). Nevertheless, they chose significantly smaller larvae for eating than for hoarding. The high mass of prey hoarded by N. fodiens (three to five times higher than in the other species) means that N. fodiens left in the nest-box only the largest items, eating all the others. This shows how subtle, exact, and effective the mechanisms of prey-size selection are.

Shrew size and prey size

The two relationships, between the size of taken and eaten prey and shrew body size and between shrew body size and specialization and preference to hunt certain prey sizes, have been supported by many examples from the wild (Abe, 1968; Aitchison, 1987; Buckner, 1964; Churchfield, 1991, 1994; Churchfield and Sheftel, 1994; Dickman, 1988; Platt and Blakley, 1973). This can be explained by the fact that bite force increases with increase in shrew body size (Carraway and Verts, 1994). Consequently, the large N. fodiens needs 2.4 times shorter time than the pigmy S. minutus to handle the same prey (Haberl, 1998). Assuming that all shrews should accept a similar handling time per item, the maximum hardness or size of prey useful for small shrews should differ from those for large shrews. Therefore, we expected that the size of utilized prey would increase with increases body size of our shrews.

The tiny *S. minutus* hoarded smaller prey items than the other shrews, the large *N. fodiens* hoarded larger prey than the other shrews, and the sizes of prey hoarded by the two medium species were in between. This is consistent with the above examples and with our prediction. But results relating to the size of prey eaten are not. The deviations are: (1) *S. araneus* ate larger prey than *Neomys anomalus* and *N. fodiens*, (2) *S. minutus* and *N. anomalus* ate prey items of similar sizes (difference was insignificant), and (3) prey eaten by *N. anomalus* and *N. fodiens* were also of similar masses (Figure 4).

The first deviation probably resulted from the fact that *S. araneus* ate more large snails than *N. anomalus* and *N. fodiens* and did not eat tiny aquatic arthropods, which were eaten in high proportions by both water shrew species (Figure 2a). Similarly, mean mass of eaten prey was higher in *S. araneus* than in *S. minutus* because *S. minutus* ate mainly small insect

larvae and avoided large earthworms and snails readily eaten by *S. araneus*.

Apparently, consumption of many aquatic arthropods caused such a reduction in the mean mass of prey eaten by *N. anomalus* that it did not differ significantly from that in *S. minutus*. As to the third deviation, *N. anomalus* and *N. fodiens* ate all prey types in similar proportions (Figure 2a). Thus, mean masses of prey eaten by these species were also similar.

Furthermore, all the three deviations can be related to the fact that species and size diversity of prey offered in our experiments were undoubtedly low (only six prey types with low variability in their masses; Table 2). In the wild, tens of prey families and hundreds of genera are simultaneously available in foraging patches (Churchfield, 1982a; Churchfield et al., 1991, 1997; Kolibáč, 1996). Also, prey diversity in shrew diets is high (Castién and Gosálbez, 1999; Churchfield, 1984, 1991, 1994; Churchfield and Sheftel, 1994). Therefore, it is probable that a higher diversity of prey types would result in a higher differentiation of mean masses of prey eaten by our shrews.

This leads to the conclusion that, in order to explain subtle interspecific differences in foraging behavior and prey preferences, laboratory experiments should be carried out with a higher prey diversity than in our study. However, such experiments will be difficult to execute and may suffer from other methodological limitations.

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