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

First author (to whom reprint requests should be sent; correspondence address = institutional affiliation):
Leszek RYCHLIK
Mammal Research Institute
Polish Academy of Sciences
17-230 Białowieża
Poland
e-mail: lrychlik@bison.zbs.bialowieza.pl
fax: 0048-85-6812289
phone: 0048-85-6812278

Second author:
Elżbieta JANCEWICZ
Department of Forest Zoology and Wildlife Management
Agricultural University SGGW
Rakowiecka 26/30
02-528 Warsaw
Poland
e-mail: jancewicz@delta.sggw.waw.pl

Running title: Prey size and quality, and food handling by shrews

Abstract

Some predictions relating metabolic constraints of foraging behavior and prey selection were tested by comparison of 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 large prey (>0.3 g). The larvae were the highly nutritious food (>8 kJ/g) and the other prey were the low nutritious food (<4 kJ/g). The smallest *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% 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 *N. fodiens* utilized the least food mass and the least energy quantity per 1 g of its body. Also, the proportion of food hoarded by shrews decreased with an increase in size. 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: foraging behavior, prey size preferences, prey energetic value, food hoarding, optimal foraging strategy, energy requirements

Introduction

Almost all soricine shrews have very 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 nine-fold 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 must lead to interspecific differences in metabolism as well as 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. On the other hand, mass-specific 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) therefore are 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). Therefore, short-term food hoarding should be more important and common in small than large shrews (Hanski, 1989, 1994; Lucas and Walter, 1991; McNamara et al., 1990; Saarikko, 1989). On the other hand, small shrews have lower ability to defend food resources and they should display a stronger tendency to scatter hoarding 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. But anyway, there are several reasons why large prey should be more suitable for hoarding than small prey (Rychlik, 1999a): (1) transportation of several large prey to the shelter is probably energetically less costly than that of many small ones; (2) few transportations of large prey expose the shrew to predation less than do multiple transportations of small ones; (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.

All the above predictions are supported by very little experimental evidence 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 papers cited 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 as 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 upon large prey and small shrews to small prey in the wild (Churchfield, 1991; Churchfield and Sheftel, 1994; Dickman, 1988). Therefore, these problems need further investigations.

Although "energy remains 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 usually lasted only up to 15 minutes (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). Therefore, longer experiments are needed.

In this study food handling and utilization were compared in four co-existing 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 hr. Since two shrew species were semiaquatic, two of six prey types were aquatic.

The following predictions were tested in this study: (1) mass-specific 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.

Material and methods

Trapping and keeping shrews in captivity

Wild shrews were trapped in the Białowieża Forest (E 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 × 40 × 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°C, and the air humidity ca. 80%.

Shrews underwent at least a 2-week-acclimatization to these conditions. During this period they could acquaint themselves 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 the plastic cages (30 × 40 × 15 cm) with a nest box (filled with cuttings of wood-wool), a sheet of white paper on the floor, and 6 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 day-time (mostly between 10.00 and 18.00), i.e. during the period of decreased feeding and locomotor activity of shrews (Buchalczyk, 1972). Tested shrews were fed with the non-test food ≥ 5 hr 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, it was assumed that shrews could feel some hunger but were not starved at the beginning of tests.

Six live prey types were used 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 large prey, whereas fly and mealworm larvae, and aquatic arthropods were small prey (Table 2). Small prey were ca. 4 times lighter than large prey (Mann-Whitney test: $U = 0.0$ to 1673.5, $p < 0.001$) and they were given in ca. 2 times higher numbers than large prey ($U = 0.0$ to 4920.0, $p < 0.001$).

Only the exact handling times for mealworms (23-28 mm long, 122.5 ± 13.0 mg of wet mass) were known: 23.7 ± 5.9 s for *N. fodiens*, 30.2 ± 5.5 s for *N. anomalus*, 33.4 ± 6.5 s for *S. araneus*, and 57.6 ± 13.1 s for *S. minutus* (Haberl, 1998). Handling times for the other prey were not measured or known from literature. However, according to their body length, hardness, escape abilities etc., 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 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, 2.9 kJ/g for snails (Ruthardt, 1990), 3.7 kJ/g for aquatic arthropods [an average value for *Asellus aquaticus* – 3.2 kJ/g (Prus, 1977) and *Gammarus* spp. – 4.2 kJ/g (Ruthardt, 1990) was accepted], and 3.0 kJ/g for small fish (Fischer, 1970). Prey were given on open trays placed one next to the other (trays covered an area of < 200 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, the shrew was placed in the test cage and left 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 hr. Immediately after the 4-hr-period the shrew was removed 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 (in order to reduce intraindividual variation) and 4 hr per day. This resulted in 12 hr of observations for each individual, 120 hr for each species, and 480 hr for all shrews.

Analysis of data

The average mass of one prey item of a given category was calculated 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. Partly eaten prey items were categorized 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 NON-UTILIZED food, whereas prey hoarded + eaten as UTILIZED food.

Next, for each shrew and each analyzed parameter, the three values from three succeeding days were averaged and first degree averages (1°) were obtained. 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: $U = 0.0$ to 11.0, $p < 0.005$). The smallest *Sorex minutus* was nearly five times lighter than the largest *Neomys fodiens* (Table 1).

With regard to prey handling (Fig. 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: $W = 55$, $p = 0.002$ for the all three comparisons). It also abandoned quite a lot of taken prey (20.9%). So, the proportion of non-utilized food (left + abandoned = 71.1%) was much higher than that of utilized food (hoarded + eaten = 28.9%; $W = 55$, $p = 0.002$).

The proportions of utilized and non-utilized 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; Fig. 1a). The two *Neomys* species ate significantly more food than hoarded, abandoned and left on trays ($W = 43$ to 55, $p = 0.027$ to 0.002). However, the proportions of non-utilized 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 (Fig. 1a).

Interspecific comparisons revealed that the two *Sorex* species left significantly more prey on trays than the two *Neomys* species (Mann-Whitney test: $U = 5.0$ to 18.0, $p = 0.001$ to 0.018). *S. araneus* abandoned significantly less prey than the three other species ($U = 11.0$ to 19.5, $p = 0.004$ to 0.024). 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, $p < 0.05$), but it ate more food than the other species (significantly more than *S. minutus*; $U = 0.0$, $p < 0.001$). *S. minutus* ate significantly less prey than the other species ($U = 0.0$ to 7.0, $p < 0.002$). *N. anomalus* and *S. araneus* hoarded and ate food in similar proportions. *S. minutus* utilized significantly less food than the three other species ($U = 8.0$ to 21.0, $p = 0.002$ to 0.032; Fig. 1a).

The analysis of prey utilization (hoarding vs. eating; Fig. 1b) showed that all species ate proportionally more food than hoarded. The smallest difference was for the tiny *S. minutus* (Wilcoxon test: $W = 45$, $p = 0.020$), whereas for the other species the differences were highly significant ($W = 55$, $p = 0.002$). There were not significant differences in prey utilization between *S. araneus* and *N. anomalus*, the two medium-size species. But the large *N. fodiens* hoarded less food than the medium-size species (significantly less than *N. anomalus*; $U = 20.0$, $p = 0.026$). In contrast, the small *S. minutus* hoarded proportionally more food than the medium shrews (significantly more than *S. araneus*; $U = 21.0$, $p = 0.032$) and much more than *N. fodiens* ($U = 9.0$, $p < 0.003$).

The prey of high energetic value (larvae of mealworms and fly) composed 80% of food eaten and 75% of food utilized by *S. minutus* (Fig. 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; Fig. 2a).

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

Mean total masses and energetic values of food eaten and utilized by shrews of particular species were also compared (Figs 2 and 3). Interspecific comparisons showed that medium-size shrews, *S. araneus* and *N. anomalus,* ate similar masses of prey (Figs 2a and 3a). Large *N. fodiens* ate significantly more food than the three other species (Mann-Whitney test: $U = 0.0$ to 19.0, $p =$ 0.001 to 0.021) and tiny *S. minutus* ate significantly less food than all the other species ($U = 0.0$ to 2.0, $p < 0.001$). 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 ($U = 2.0$ to 7.5, $p < 0.002$), and *N. fodiens* utilized more food than the other species (but the difference was significant only between *N. fodiens* and *S. minutus*; $U = 2.0$, $p < 0.001$; Figs 2b and 3d).

Smaller shrews, on average, ate and especially utilized more food per unit of body mass than larger shrews (Fig. 3b and 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 (Fig. 3c and f), the only significant differences were between *S. minutus* and the two *Neomys* species (U = 17.0, p = 0.014 for mass-specific energy consumption and U = 8.0 and 18.0, p < 0.002 and 0.018 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 (Fig. 3c and f).

Except *S. araneus*, all shrews hoarded significantly larger prey items than those which they ate (Wilcoxon test: W = 28 to 43, p = 0.039 to 0.016; Fig. 4). Pigmy *S. minutus* hoarded significantly smaller prey than the three other species (Mann-Whitney test: U = 0.0 to 17.0, p = 0.001 to 0.02). This species also ate smaller prey than the other shrews (significantly smaller than *S. araneus* and *N. fodiens*; U = 4.0 and 10.0, p < 0.001 and 0.003, respectively). The large *N. fodiens* hoarded significantly larger prey than the other species (U = 0.0 to 5.5, p < 0.001 to 0.005), but it ate prey of similar size as *N. anomalus* did, smaller than *S. araneus* (U = 17.0, p = 0.014), and larger only than *S. minutus* (U = 10.0, p < 0.003). 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 to 17.0, p = 0.001 to 0.014; Fig. 4).

Discussion

In other studies (Churchfield, 1982; 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 of wet mass of prey per 4 hr. We offered on average 6.7 g of prey per 4 hr. 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 it was expected, per capita food consumption (as well as utilization) increased with an increase in shrew body mass. These results are not very revelational, but so far there has not been clear and methodologically correct experimental evidence for this relationship in shrews.

Hanski (1994) suggests that large shrews (body mass ≥ 10 g) have ca. 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 (Fig. 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* (Fig. 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 (Fig. 2) which contained 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 2 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 to 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 Jowell, 1962; Köhler, 1984; Rychlik L., pers. obs.). 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, among others, 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, it usually is “a suite of responses (...) both to environmental quality and current physiological state” (Lucas, 1994). In shrews it 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 shrew 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).

Surprisingly, 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 interspecfic 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. Simultaneously, the fact that *N. anomalus* hoarded proportionally more prey than *S. araneus* (rather an inverse tendency was expected according to their masses) can be explained: the level of trophic specialization is probably higher in *N. anomalus* than in *S. araneus*.

Size of hoarded vs. eaten prey

As it was 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 which display a tendency to eat small food items at once and hoard large ones (see Rychlik, 1999a).

The four reasons why large prey should be more suitable for hoarding than small prey are listed in the Introduction. Since 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 that of small prey and (2) big prey were probably more resistant to decaying than the small ones. However, the tendency can partly resulted from the possibility that some hoarded prey were items left by shrews in nest boxes because they needed too long time to be eaten. For example, long and resilient earthworms (hoarded by all shrews except *N. fodiens* – Fig. 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. On the other hand, 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 mice flesh and insects (easier to manipulate) before hard sunflower seeds (Martin, 1984); 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 very high mass of prey hoarded by *N. fodiens* (3-5 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: (1) the size of taken and eaten prey increase with an increase in shrew body size and (2) large shrews display some specialization and preference to hunt upon large prey, whereas small shrews to small prey, 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 increase with an 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 the increase in 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 our prediction. But results relating to the size of prey eaten are not. The deviations lie in: (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), (3) prey eaten by *N. anomalus* and *N. fodiens* were also of similar masses (Fig. 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 (Fig. 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 (Fig. 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, 1982; Churchfield et al., 1991, 1997; Kolibáč, 1995). Also, prey diversity in shrew diets is high (Castién and Gosálbez, 1999; Churchfield, 1984, 1991, 1994; Churchfield and Sheftel, 1994). Therefore, it is very 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, the laboratory experiments should be carried out with a higher prey diversity than in our study. However, such experiments will be very difficult to execute and may suffer from other methodological limitations.

Acknowledgements: We are very grateful to Z. Pucek for enabling this study and scientific supervision; to A. Arasim, A. Buszko and S. Buszko for field and technician assistance; to J. Gliwicz and J. R. E Taylor for critical comments on earlier versions of the manuscript; to N. Downs for correction of our English.

References

Abe H, 1968. Classification and biology of Japanese Insectivora (Mammalia). II. Biological aspects. J Facul Agricult, Hokkaido Univ 55:429-458.

Aitchison CW, 1987. Review of winter trophic relations of soricine shrews. Mammal Rev 17:1-24.

Andersson M, Krebs J, 1978. On the evolution of hoarding behaviour. Anim Behav 26:707-711.

Barnard CJ, Brown CAJ, 1981. Prey size selection and competition in the common shrew (*Sorex araneus*). Behav Ecol Sociobiol 8:239-243.

Barnard CJ, Brown CAJ, 1985. Competition affects risk-sensitivity in foraging shrews. Behav Ecol Sociobiol 16:379-382.

Barnard CJ, Brown CAJ, Gray-Wallis J, 1983. Time and energy budgets and competition in the common shrew (*Sorex araneus* L.). Behav Ecol Sociobiol 13:13-18.

Barnard CJ, Hurst JL, 1987. Time constraints and prey selection in common shrews *Sorex araneus* L. Anim Behav 35:1827-1837.

Brooks SJ, Calver MC, Dickman CR, Meathrel CE, Bradley JS, 1996. Does intraspecific variation in the energy value of a prey species to its predators matter in studies of ecological energetics? A case study using insectivorous vertebrates. Ecoscience 3:247-251.

Buchalczyk A, 1972. Seasonal variations in activity of shrews. Acta Theriol 17:221-243.

Buckner CH, 1964. Metabolism, food capacity and feeding behaviour in four species of shrews. Can J Zool 42:259-279.

Carraway LN, Verts BJ, 1994. Relationship of mandibular morphology to relative bite force in some *Sorex* from western North America. In: Advances in the biology of shrews (Merritt JF, Kirkland GL, Jr, Rose RK, eds). Pittsburgh: Special Publication of Carnegie Museum of Natural History No. 18:201-210.

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. Subterranean foraging and burrowing activity of the common shrew. Acta Theriol 25:451-459.

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

Churchfield S, 1982. The influence of temperature on the activity and food consumption of the common shrew. Acta Theriol 27:295-304.

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

Churchfield S, 1990. The natural history of shrews. Bromley: Christopher Helm (Publishers) Ltd.

Churchfield S, 1991. Niche dynamics, food resources, and feeding strategies in multispecies communities of shrews. In: The biology of the Soricidae (Findley JS, Yates TL, eds). Albuquerque: The Museum of Southwestern Biology, University of New Mexico; 23-34.

Churchfield S, 1993. Foraging strategies of shrews: interactions between small predators and their prey. Symp Zool Soc Lond 65:235-252.

Churchfield S. 1994. Foraging strategies of shrews, and the evidence from field studies. In: Advances in the biology of shrews (Merritt JF, Kirkland GL, Jr, Rose RK, eds). Pittsburgh: Special Publication of Carnegie Museum of Natural History No. 18:77-87.

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

Churchfield S, Sheftel BI, 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 BI, Moraleva NV, Shvarts EA, 1997. Habitat occurrence and prey distribution of a multi-species community of shrews in the Siberian taiga. J Zool, Lond 241:55-71.

Crowcroft WP, 1955. Notes on the behaviour of shrews. Behaviour 8:63-80.

Dehnel A, 1961. Aufspeicherung von Nahrungsvorräten durch *Sorex araneus* Linnaeus 1758. Acta Theriol 4:265-268.

Dickman CR, 1988. Body size, prey size, and community structure in insectivorous mammals. Ecology 69:569-580.

Fischer Z, 1970. The elements of energy balance in grass carp (*Ctenopharyngodon idella* Val.). Part I. Pol Arch Hydrobiol 17(30):421-434.

Formanowicz DRJ, Bradley PJ, Brodie EDJ, 1989. Food hoarding by the least shrew (*Cryptotis parva*): intersexual and prey type effects. Am Midl Nat 122:26-33.

Fryxell JM, Lundberg P, 1994. Diet choice and predator-prey dynamics. Evol Ecol 8:407-421.

Genoud M, 1988. Energetic strategies of shrews: ecological constraints and evolutionary implications. Mammal Rev 18:173-193.

Haberl W, 1998. Prey handling times and partial prey consumption in five species of European shrews (Soricidae, Insectivora). Pakistan J Biol Sci 1:53-54.

Hamilton WJ, 1930. The food of the Soricidae. J Mammal 11:26-39.

Hamilton WJ, 1944. The biology of the little short-tailed shrew *Cryptotis parva*. J Mammal 25:1-7.

Hanski I, 1984. Food consumption, assymilation and metabolic rate in six species of shrew (*Sorex* and *Neomys*). Annls Zool Fenn 21:157-165.

Hanski I, 1985. What does a shrew do in an energy crisis? In: Behavioural ecology. Ecological consequences of adaptive behaviour. The 25th Symposium of the British Ecological Society, Reading 1984 (Sibly RM, Smith RH, eds). Oxford: Blackwell Scientific Publications; 247-252.

Hanski I, 1989. Habitat selection in a patchy environment: individual differences in common shrews. Anim Behav 38:414-422.

Hanski I, 1992. Insectivorous mammals. In: Natural enemies. The population biology of predators, parasites and diseases (Crawley MJ, ed). Oxford: Blackwell Scientific Publications; 163-187.

Hanski I, 1994. Population biological consequences of body size in *Sorex*. In: Advances in the biology of shrews (Merritt JF, Kirkland GL, Jr, Rose RK, eds). Pittsburgh: Special Publication of Carnegie Museum of Natural History No. 18:15-26.

Hawkins AE, Jewell PA, 1962. Food consumption and energy requirements of captive British shrews and the mole. Proc Zool Soc Lond 138:137-155.

Innes DGL, 1994. Life histories of the Soricidae: a review. In: Advances in the biology of shrews (Merritt JF, Kirkland GL, Jr, Rose RK, eds). Pittsburgh: Special Publication of Carnegie Museum of Natural History No. 18:111-136.

Jenkins SH, Breck SW, 1998. Differences in food hoarding among six species of heteromyid rodents. J Mammal 79:1221-1233.

Köhler D, 1984. Zum Verhaltensinventar der Wasserspitzmaus (*Neomys fodiens*). Säugetierkd Inform, Jena 2:175-199.

Kolibáč J, 1996. The diets of *Sorex araneus* and *Sorex minutus* in selected habitats in the Czech Republic. Acta Mus Morav, Scient nat 80:95-161.

Kotler BP, Brown JS, Hickey M, 1999. Food storability and the foraging behavior of fox squirrels

(*Sciurus niger*). Am Midl Nat 142:77-86.

Krebs JR, Erichsen JT, Webber MI, Charnov EL, 1977. Optimal prey choice in the great tit. Anim Behav 25:30-38.

Leaver L, Daly M, 1998. Effects of food preference on scatter-hoarding by kangaroo rats (*Dipodomys merriami*). Behaviour 135:823-832.

Lucas JR, 1994. Regulation of cache stores and body mass in Carolina chickadees (*Parus carolinensis*). Behav Ecol 5:171-181.

Lucas JR, Walter LR, 1991. When should chickadees hoard food? Theory and experimental results. Anim Behav 41:579-601.

McNamara JM, Houston AI, Krebs JR, 1990. Why hoard? The economics of food storing in tits, *Parus* spp. Behav Ecol 1:12-23.

Martin IG, 1984. Factors affecting food hoarding in the short-tailed shrew *Blarina brevicauda*. Mammalia 48:65-71.

Okhotina MV, 1974. The role of shrews (*Sorex*, Insectivora) in the biogeocenoses of the coniferous broad-leaved forests in Primorye Trritory. In: Therilogy (Vorontsov NN, ed). Novosibirsk: Nauka - Sibirskoe Otdelenie: 253-258.

Pierce GJ, Ollason JG, Speirs DC, 1993. Diet selection by common shrews *Sorex araneus* in a depleting environment. Behav Process 29:65-84.

Pinowski J, Drożdż A, 1968. Estimation of food preferences. In: Methods of ecological bioenergetics (Grodziński W, Klekowski RZ, eds). Warszawa: Polish Academy of Sciences; 207-214.

Platt WJ, Blakley NR, 1973. Short-term effects of shrew predation upon invertebrate prey sets in prairie ecosystems. Proc Iowa Acad Sci 80:60-66.

Prus T, 1977. Experimental and field studies on ecological energetics of *Asellus aquaticus* L. (Isopoda). IV. Energy budget of a population in the littoral zone of Powsińskie Lake. Ekol pol, A 25:593-623.

Rechten C, Avery M, Stevens A, 1983. Optimal prey selection: why do great tits show partial preferences? Anim Behav 31:576-584.

Robinson DE, Brodie ED, 1982. Food hoarding behaviour in the short-tailed shrew *Blarina brevicauda*. Am Midl Nat 108:369-375.

Ruthardt M, 1990. Ein Öko-ethologischer Ansatz zur Erklärung der semiaquatischen Lebensweise der Wasserspitzmaus (*Neomys fodiens* Pennant, 1771) (Dissertation zur Erlangung des Doktorgrades der Naturwissenschaften). Osnabrück: Universität Osnabrück.

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

Rychlik L, 1999a. Changes in prey size preferences during successive stages of foraging in the Mediterranean water shrew *Neomys anomalus*. Behaviour 136:345-365.

Rychlik L, 1999b. Food handling by the gregarious Mediterranean water shrew *Neomys anomalus*. Folia Zool 48:161-172.

Saarikko J, 1989. Foraging behaviour of shrews. Annls Zool Fenn 26:411-423.

Sih A, Christensen B, 2001. Optimal diet theory: when does it work, and when and why does it fail? Anim Behav 61:379-390.

Sorenson MW, 1962. Some aspects of water shrew behaviour. Am Midl Nat 68:445-462.

Taylor JRE, 1998. Evolution of energetic strategies in shrews. In: Evolution of shrews (Wójcik JM, Wolsan M, eds). Białowieża: Mammal Research Institute, Polish Acad Sciences; 309-346.

Vander Wall SB, 1990. Food hoarding in animals. Chicago: The University of Chicago Press.

Vogel P, 1980. Metabolic levels and biological strategies in shrews. In: Comparative physiology: primitive mammals (Schmidt-Nielsen K, Bolis L, Taylor CR, eds). Cambridge: Cambridge University Press; 170-180.

Vogel P, Bodmer C, Spreng M, Aeschimann J, 1998. Diving capacity and foraging behaviour of the water shrew (*Neomys fodiens*). In: Behaviour and ecology of riparian mammals (Dunstone N, Gorman ML, eds). Cambridge: Cambridge University Press; 31-47.

Ydenberg R, Hurd P, 1998. Simple models of feeding with time and energy constraints. Behav Ecol 9:49-53.

Yudin BS, 1962. [Ecology of shrews (genus *Sorex*) of western Siberia]. In: [Problems on the ecology, zoogeography and systematics of animals] (Yudin BS, ed). Trudy Biologicheskogo Instituta Sibirskogo Otdeleniya AN SSSR 8:33-134. [In Russian]

Table 1. Mean (± 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]	BMR [ml O_2/g×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

Table 2. Mean (± 1 SE) numbers and masses (in g) of prey offered to shrews per one ”cafeteria test” (*n* = 120 tests).

Prey type	Number of items	Mass of all items	Mass of one item
Fly larvae (L)	9.98 ± 0.01 E,S,F*	0.86 ± 0.01 E,S,A,F	0.09 ± 0.00 E,S,F
Mealworm larvae (M)	10.00 ± 0.00 E,S,F	0.86 ± 0.03 E,S,A,F	0.09 ± 0.00 E,S,F
Earthworms (E)	4.11 ± 0.09 L,M,S,A,F	1.52 ± 0.05 L,M,S,A,F	0.38 ± 0.01 L,M,A,F
Snails** (S)	5.00 ± 0.00 L,M,E,A,F	1.91 ± 0.10 L,M,E,A,F	0.38 ± 0.02 L,M,A
Aquatic arthropods (A)	9.79 ± 0.47 E,S,F	0.48 ± 0.02 L,M,E,S,F	0.08 ± 0.01 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

* Within columns, significant differences (Mann-Whitney test: $p < 0.05$) 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).

** Mass of shells included.

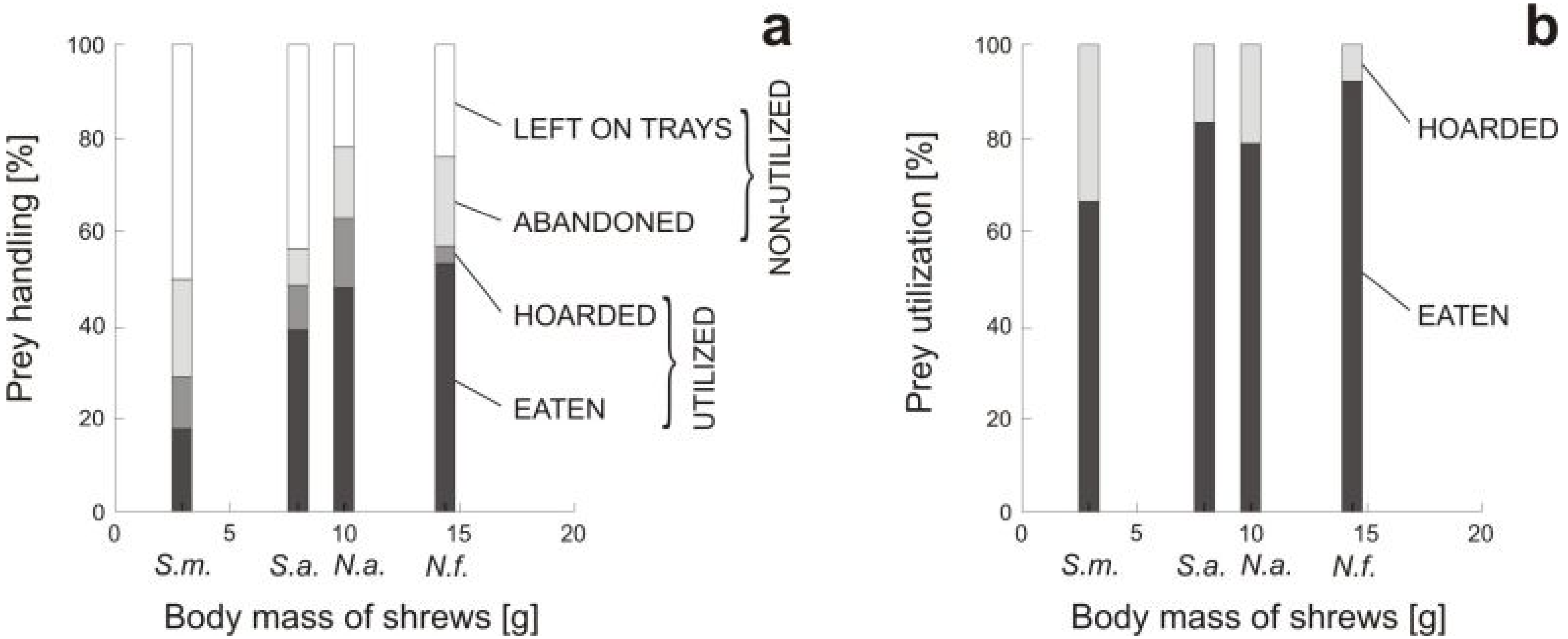

Fig. 1. Prey handling (a) and utilization (b) by the four shrew species of different body masses. Distinguished categories: EATEN - proportion of prey items eaten by shrews, HOARDED - prey hidden in the nest box, ABANDONED - prey abandoned in the cage out of the nest box, LEFT ON TRAYS - prey not taken. 100% = numbers of all items given at the beginning of particular test (a) or number of items eaten and hoarded during particular test (b).

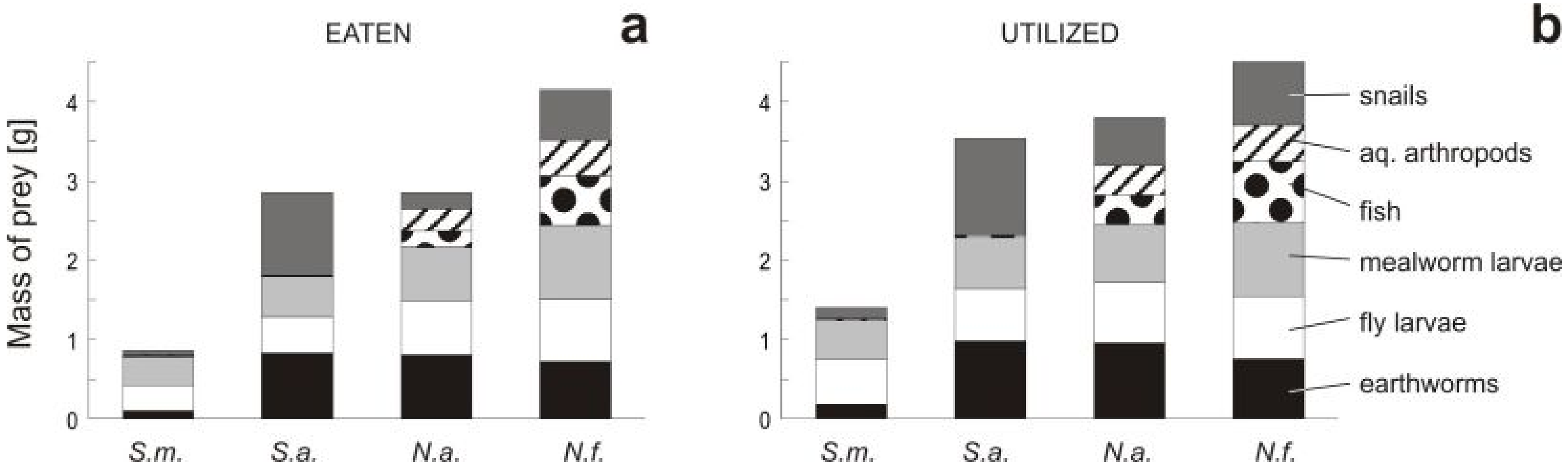

Fig. 2. Masses of particular prey types eaten (a) and utilized (b) by the four species of shrew. Species abbreviations as in Fig. 1.

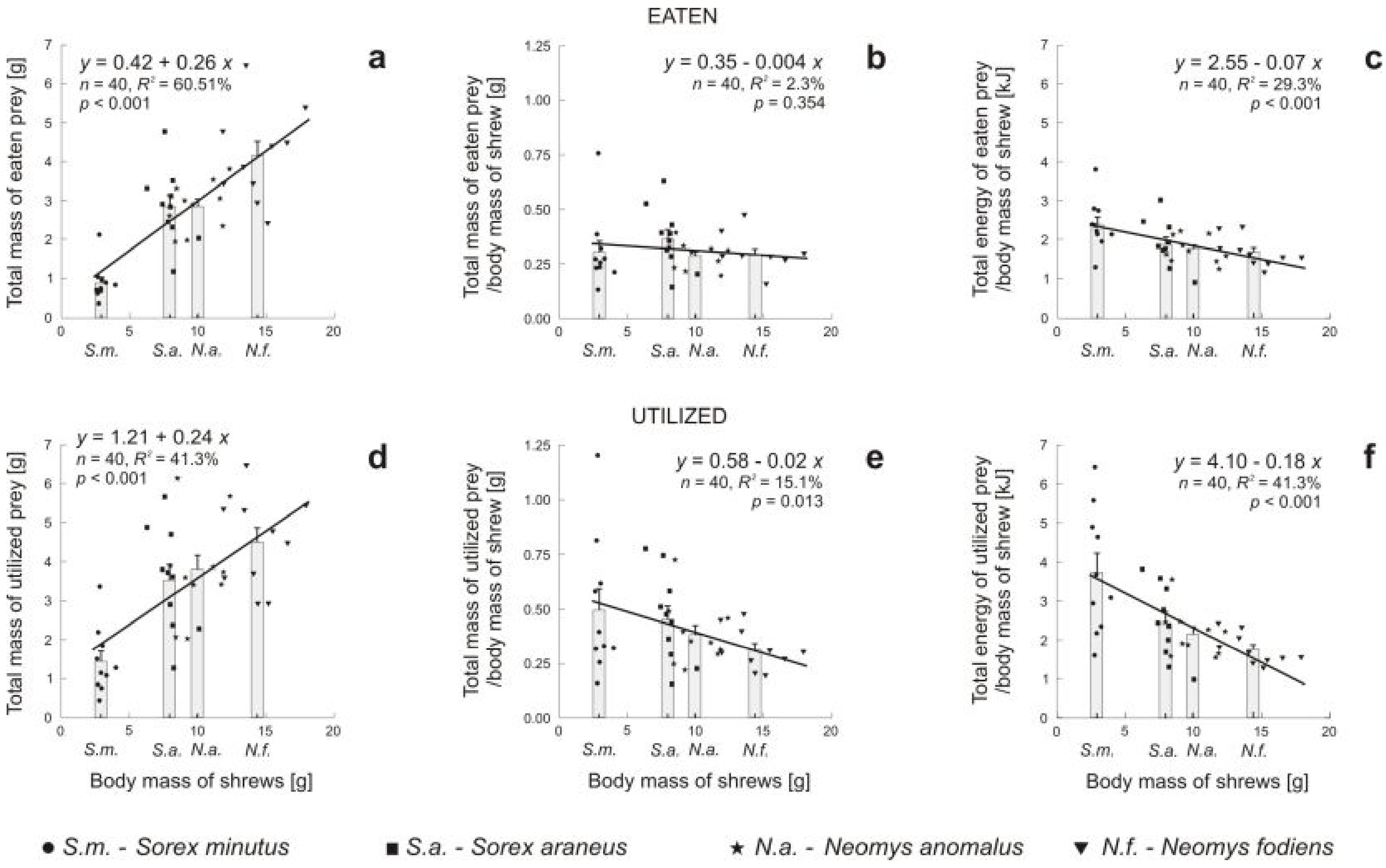
EATEN
a
y = 0.42 + 0.26 x
n = 40, R² = 60.51%
p < 0.001
Total mass of eaten prey [g]
b
y = 0.35 - 0.004 x
n = 40, R² = 2.3%
p = 0.354
Total mass of eaten prey /body mass of shrew [g]
c
y = 2.55 - 0.07 x
n = 40, R² = 29.3%
p < 0.001
Total energy of eaten prey /body mass of shrew [kJ]
UTILIZED
d
y = 1.21 + 0.24 x
n = 40, R² = 41.3%
p < 0.001
Total mass of utilized prey [g]
e
y = 0.58 - 0.02 x
n = 40, R² = 15.1%
p = 0.013
Total mass of utilized prey /body mass of shrew [g]
f
y = 4.10 - 0.18 x
n = 40, R² = 41.3%
p < 0.001
Total energy of utilized prey /body mass of shrew [kJ]
S.m. S.a. N.a. N.f.
Body mass of shrews [g]
● S.m. - Sorex minutus
■ S.a. - Sorex araneus
★ N.a. - Neomys anomalus
▼ N.f. - Neomys fodiens

Fig 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.

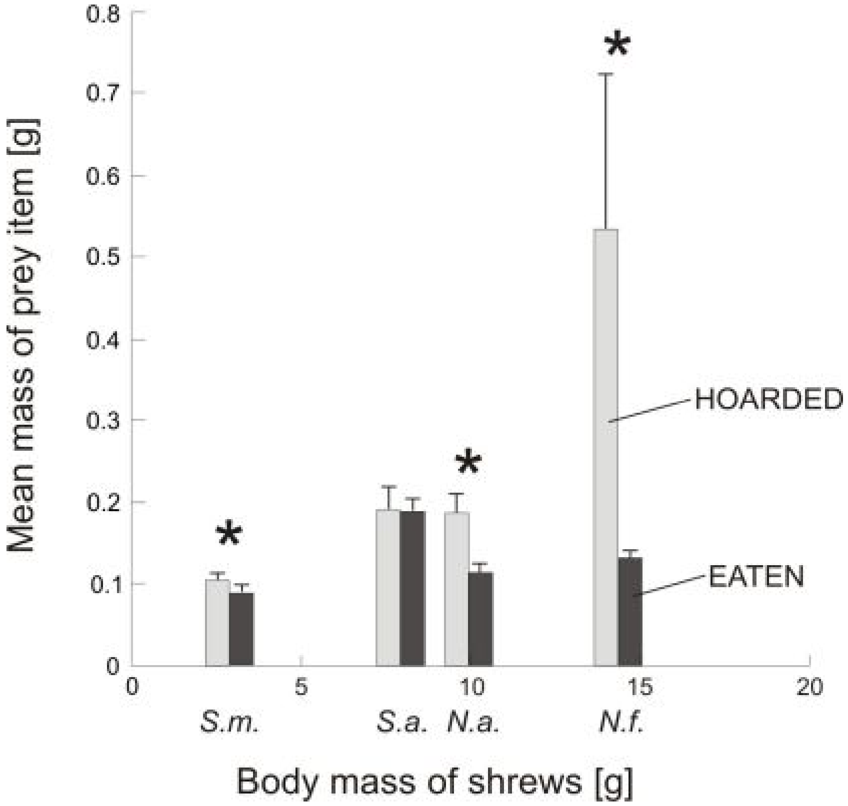

Fig. 4. Mean (+ 1 SE) masses of prey items hoarded and eaten by the four shrew species of different body masses. Intraspecific significant differences (Wilcoxon test: $p < 0.05$) between categories are indicated by asterisks. Species abbreviations as in Fig. 1.