Differences in swimming and diving abilities between two sympatric species of water shrews: *Neomys anomalus* and *N. fodiens* (Soricidae)

Helena MENDES-SOARES[1, 2] and Leszek RYCHLIK[1, 3]

Helena MENDES-SOARES, [1]Mammal Research Institute of the Polish Academy of Sciences, Waszkiewicza 1, 17-230 Białowieża, Poland; [2]present address: Department of Biology, Indiana University, Bloomington, Jordan Hall A308, 1001, East Third St., Bloomington, IN 47405, U.S.A., e-mail: mhmendes@indiana.edu

Leszek RYCHLIK, [1]Mammal Research Institute of the Polish Academy of Sciences, Waszkiewicza 1, 17-230 Białowieża, Poland; [3]present address: Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznań, Poland, e-mail: lrychlik@amu.edu.pl

19 text pages, 1 table and 4 figures

corresponding address:

Prof. UAM Dr. hab. Leszek RYCHLIK
Institute of Environmental Biology
Faculty of Biology
Adam Mickiewicz University
Umultowska 89
61-614 Poznań
Poland
e-mail: lrychlik@amu.edu.pl or rychliklesz@gmail.com
tel.: (+4861) 829-57-51
fax: (+4861) 829-56-36

Abstract

Swimming and diving abilities of two syntopic species of water shrews, *Neomys anomalus* and *N. fodiens*, were tested in aquaria using video-recordings taken from three views (lateral distant, lateral close and dorsal). The frequency and total duration of diving, as well as the mean duration of diving and floating bouts, were significantly higher in *N. fodiens* than in *N. anomalus*. Frequency of paddling during surface swimming was lower in *N. fodiens* than in *N. anomalus*. *N. fodiens* dived mainly for long distances at the bottom of the aquarium and performed a wider range of dive profiles than *N. anomalus*, which preferred rather short and shallow dives. The two species differed also significantly in their Fineness Ratios (describing how streamlined their bodies are) when diving. When swimming, *N. fodiens* had a relatively wider body and performed narrower movements with its tail than *N. anomalus*. These results show quantitatively and qualitatively for the first time that *N. fodiens* is more proficient at swimming and diving than *N. anomalus*. The results also help to explain the interspecific differences in efficiency of underwater foraging, and support the idea of segregation of ecological niches of these species based on their different foraging modes (diving vs wading).

Key words: foraging behaviour; interspecific competition; microhabitat selection; underwater foraging; water shrews

Introduction

Neomys anomalus and *Neomys fodiens* are two species of water shrews that live mainly along small water courses and ponds, and in swamps and marshy meadows (Rychlik 2000). Although the distribution of *N. anomalus* may be conditioned by the presence of *N. fodiens* (Torre and Tella 1994; Kryštufek et al. 2000), they occur sympatrically and syntopically in many areas (Spitzenberger 1990, 1999; Rychlik 1997, 2000). Therefore, their ecological niches overlap in different dimensions (Rychlik 2000, 2005; Churchfield and Rychlik 2006) and they compete for food resources and life space (Rychlik 1997, 2004; Rychlik and Zwolak 2005, 2006). However, in many places they coexist for a long time, so some mechanisms separating their niches must be present.

Both species have morphological adaptations (feet and toes with fringes of stiff hairs, tail with keel, reduced ears, closeable nostrils) to their semi-aquatic life mode (Hutterer 1985; Pucek 1981; Churchfield 1998). The pelage of water shrews is also denser than that of terrestrial shrews and the awn hairs possess an H-shaped profile with lateral ridges filled with numerous ridges, which is believed to retain air, providing better insulation and buoyancy (Churchfield 1998). Although *N. anomalus* is strongly associated with water, its fringes of stiff hairs on the feet and the keel on the tail are less prominent than in *N. fodiens* (Pucek 1981; Churchfield 1998). In the wild, *N. anomalus* prefers places flooded with shallow water, whereas *N. fodiens* prefers those with direct access to streams and deep water (Rychlik 2000). The diet of *N. anomalus* is composed only or mostly of terrestrial prey (Niethammer 1978; Kuvikova 1985a, 1987; Churchfield and Rychlik 2006), whereas up to 95% of the diet of *N. fodiens* may be composed of aquatic prey (Niethammer 1978; DuPasquier and Cantoni 1992). All these attributes suggest better swimming and diving abilities in *N. fodiens* than in *N. anomalus*.

These abilities, as well as underwater hunting tactics or learning skills, have been investigated several times in *N. fodiens* (e.g. Ruthardt and Schröpfer 1985; Köhler 1991, 1993, 1996; Haberl 1993; Vogel et al. 1998). Ruthardt and Schröpfer (1985) described two underwater hunting tactics for this species: in open water for pelagic prey and at the bottom for benthic prey. *N. fodiens* was able to improve its food finding in underwater bowls and mazes through trial-and-error learning (Köhler 1993, 1996). Its maximal diving depth was 260 cm and the number of dives per day exceeded 520 (Vogel et al. 1998). Except for the work of Haberl (1993), these abilities had not previously been examined in *N. anomalus*, enhancing the need for the present study.

The aim of this work was, therefore, to analyse and compare qualitatively and quantitatively the swimming and diving behaviour of *N. anomalus* and *N. fodiens* in captivity. In the previous study (Rychlik 1997) it was shown that success and effectiveness of underwater foraging are higher in *N. fodiens* than *N. anomalus*. In the present study, we were interested in answering a question why the two species differed in success and effectiveness of underwater foraging, i.e. in finding mechanistic differences (e.g. in swimming velocity, stroking frequency, body inclination, fineness ratio or diving profiles) responsible for more efficient swimming and diving in one species than in another. For this purpose, simple experimental conditions (e.g. aquaria without resting places, aquatic prey or opportunity for spontaneous swimming) seemed to be good enough. We adopted the hypothesis that *N. fodiens* swims and dives more efficiently than *N. anomalus* and, based on theoretical works (Fish 1993b; Biewener 2003), tested the following predictions: (a) during surface swimming, the angle between the body and water surface will be smaller in *N. fodiens* than in *N. anomalus*, (b) velocity of swimming will be higher in *N. fodiens*, (c) body of *N. fodiens* will be more streamlined, (d) *N. fodiens* will generally spend more time diving, and (e) the duration of diving bouts will be longer in *N. fodiens* and they will swim a longer distance underwater. It was also assumed that the differences found would help to explain the mechanisms of resource partitioning and separation of ecological niches among these shrews.

Material and methods

Tested animals (10 individuals of *N. anomalus* and 9 of *N. fodiens*; all subadult, i.e. fully grown but sexually inactive) were trapped in wet habitat around Białowieża village (Narewka River valley, eastern Poland) from August to November, 2003 and 2004. They were kept for 1 to 5 months in the laboratory of the Mammal Research Institute PAS (MRI) in Białowieża, under a natural light-and-dark cycle, 15-20ºC and humidity ca. 80%. Each shrew was kept in an individual cage (38 × 30 × height 16 cm) equipped with a shelter (reversed pot filled with moss) and litter (a mixture of sand, sawdust, peat, and moss). Water and food (minced beef, fly larvae, dried *Gammarus* sp.) were given *ad libitum*. Sample size was increased with 1 individual of *N. anomalus* and 3 of *N. fodiens* studied by LR in 1992 at the University of Osnabrück (Germany) under similar conditions of captivity and regime of handling and filming.

Procedure of experiments

Experiments were carried out between 16:00 and 20:00 in the laboratory, using two aquaria to analyse different behaviours. One large aquarium (100 × 30 × height 40 cm) was used for lateral distant and lateral close recordings, with the filming being done from one of the long sides of the aquarium. This aquarium had ca. 3 cm of pebbles on the bottom and a water depth of 25 cm. The other aquarium (60 × 30 × height 30 cm; water depth 20 cm) was used for dorsal-view recordings. Both aquaria had a 1 × 1 cm grid on the background wall. The temperature of air and water was ca. 18ºC.

Experiments with each animal consisted of 1-5 trials (usually 5) and each trial consisted of three 5-minute recordings of the three different types performed in a random order. The animals were placed in the aquaria on a starting platform (a movable plastic shelf at one of the shorter sides) for 15-30 seconds, and were induced to swim by slowly lowering the platform under the water. Between the lateral distant and lateral close recordings, the animals were allowed to rest on the starting platform for approximately 2 minutes and given a small piece of minced meat (no food was in water). Between the lateral and dorsal recordings, the shrews were transferred to their cages where they remained from 30 minutes to a few days. To keep the water-repellent nature of the fur intact, animals were carried in a wooden box or held by the tail with forceps (i.e. their fur was not handled) during transfer to and from the test aquaria. This way, the animals' fur was sufficiently dry on all the trials performed. Each animal was submitted to one trial per day but was tested 1-5 times (usually 5 times during 5 successive days). Every few trials, the walls of aquaria were cleaned and the water partially replaced.

The behaviour of the water shrews was recorded using a Digital Video Camera Sony DCR-VX2000 E. The camera was programmed with AES program, a shutter speed of 6000 and a manual focus of the closest views for better image quality. During filming, two lamps of 75 and 150 watts were placed on the sides of the aquaria.

Data analysis

The recordings were transposed (with Broadway ver. 5.1 software) to digital format (.jpg and .mpeg) and the files were analysed frame-by-frame (25 frames/sec) using Corel Photo-Paint 9® and Corel Draw 9®. The following categories of behaviour were distinguished: (a) swimming - the animal actively used its paws to move on the water surface; (b) floating - the animal stayed on the water surface but did not move or used its paws only for balance; (c) diving - the animal moved with its whole body under water. The following features of each behaviour were analysed from the different view recordings, with an accuracy of 0.04 s (1 frame) for duration, 1 cm for distance and 0.1 degrees for angle:

1) Lateral distant view: (a) proportion of behaviours - proportion of each behaviour (floating, swimming and diving) in the total duration of the recording; (b) swimming speed

– measured as the distance swam by the animals during 1 second; (c) diving profiles (see below for definition); and (d) duration of each diving bout.

2) Lateral close view: (a) stroke frequency of paddling – number of strokes performed by one hind limb in 1 second during surface swimming; (b) inclination – the angle maintained between the central long axis of the animal's body and the water line; (c) duration of each floating bout; (d) duration of each diving bout; (e) the Fineness Ratio – maximum length to maximum height of the body (the measure of streamlining - Fish 1993b; Fig. 1) while swimming, diving and floating; and (f) the diving profiles (see below).

3) Dorsal view: (a) width of body as compared to amplitude of tail beating – maximum width of body to maximum amplitude of the tail beating at the same moment; (b) width of the body as compared to its length.

Profiles. The diving profiles performed by shrews were classified according to 16 models (Fig. 2). These were *a priori* idealized according to four factors and a score was given according to an assumed quantity of energy expended for each action (1 for lower or 2 for higher energetic cost; for scores see Fig. 2): (a) descent angle - obtuse vs acute; (b) depth of the dive - shallow (up to the half of the water depth, i.e. ca. 12 cm) vs deep (more than 12 cm, usually to the bottom); (c) distance swum underwater reaching the deepest point - short (up to 25 cm) vs long (more than 25 cm); and (d) ascent angle - obtuse vs acute. The scores of each profile were added for these factors and three difficulty categories were established: easy - total score of 4 or 5 (profiles P1–P5), medium - total score of 6 (profiles P6-P11) and difficult - total score of 7 or 8 (P12-P16). The real dives of water shrews, of course, did not have to start at left edge of aquarium (as shown in Fig. 2) but could start at any point of water surface. Not only straight-line but also curve-line dives were included into the analysis.

Data organization. Except for the diving profiles, data for each analysed parameter underwent 3-gradual averaging: 1st° average was calculated for a given trial, 2nd° average for each tested shrew (including up to 5 trials), and 3rd° average for species (up to 12 shrews). The 3rd° averages are shown in the table and figures, whereas the 2nd° averages were used in statistical analyses as replications. This data manipulation was done in order to reduce intra- and interindividual variation and avoid pseudo-replication.

Statistical analysis. Mann-Whitney *U*-test was used (with STATISTICA ver. 6) for interspecific statistical comparisons of all behaviours except the diving profiles. Distributions of frequencies of different types of profiles were compared by Kolmogorov-Smirnov test (SYSTAT ver. 5; Sokal and Rohlf 1995). This informed us about the significance of general differences between the species as well as differences between the observed and expected distributions within each species. We assumed that the shrews would not display preference for any particular profile, so the observed frequency would be close to an expected uniform distribution with frequencies of each profile type = 6.25 (100% × 1/16 = 6.25). Replicated goodness-of-fit tests (*G*-statistic) (Sokal and Rohlf 1995) were performed to compare the total number of dives and the number of difficult dives performed by each species, as well as in pairwise comparisons of each diving profile. Statistical significance was considered at $p < 0.05$ (two-tailed). Some behaviours were not displayed by or measurable in all tested animals, therefore the sample size n differs usually from 11 in *N. anomalus* and 12 in *N. fodiens.*

Ethical note

The animals were cared for in accordance with the *Guidelines for the treatment of animals in behavioural research and teaching* (Anonymous 2003). Pregnant and lactating females (as well as other unwanted small mammals) were immediately released at the place of capture. The duration of the tests (= 5-minute-recordings) was chosen after considering the experiments performed by Vogel (1990), in which animals were forced to swim or dive for 6 minutes. The tests were carefully monitored and were stopped if any animal showed an apparent difficulty in staying afloat. This happened to only one animal, and when the experiment with this animal restarted the following day, the animal did not show any signs of difficulty or extreme stress. None of the animals died during or directly after a test. We have obtained permission (no. DLOPiKog. 4201-04-136/2001/2002 of 28 February 2002) from the Minister of Environment for our capturing of the protected shrews and an acceptance (no. 2001/11 of 11 January 2001) from the Local Ethical Commission for Experiments with Animals in Białystok (Poland) for our experimental methods.

Results

The proportions of different behaviours varied between the species (Fig. 3). Both species spent most of their time swimming (ca. 92% for *N. anomalus* and 80% for *N. fodiens*), but this time was significantly longer in *N. anomalus* than in *N. fodiens* (Mann-Whitney U-test: $U = 6.0$, $p = 0.003$). Shrews swam all over the aquarium but preferred to stay near the walls and corners. The duration of floating did not differ between species ($U = 21.0$, $p = 0.149$). While floating the animals would scratch themselves, groom their fur or look around the aquarium. The time spent diving was significantly ($U = 4.0$, $p = 0.002$) shorter in *N. anomalus* than *N. fodiens*.

Surface behaviours

The speed of surface swimming did not differ significantly between species ($U = 40.0$, $p = 0.965$; Table 1), but the stroking frequency of paddling was higher in *N. anomalus* than *N. fodiens* ($U = 22.5$, $p = 0.013$). The animals paddled with an alternate stroking of the front and hind limbs on a transverse plane. The inclination of swimming animals from horizontal was quite low for both species and did not differ significantly ($U =$

36.0, p = 0.305). In both species the nose and head were always just above the water surface and the tail undulated on or near the surface (Fig. 1). The ratio of the maximum width of the body to the maximum amplitude of the tail movement was significantly higher in *N. fodiens* than in *N. anomalus* (U = 3.0, p = 0.004), indicating that *N. fodiens* performed narrower movements with the tail. However, *N. fodiens* had a significantly wider body (U = 3.0, p = 0.004) in comparison to *N. anomalus*.

The mean duration of single floating bouts was significantly longer in *N. fodiens* than in *N. anomalus* (U = 12.0, p = 0.012; Table 1). To float, the animals would project their limbs downwards and their body would be less stretched; the tail appeared to float without any active effort from the animal. The Fineness Ratio (FR) while floating was quite low for both species (Table 1) and no significant interspecific difference existed (U = 17.0, p = 0.855). Also when swimming, the FR did not differ significantly between the species (U = 51.0, p = 0.356).

Diving behaviour

The interspecific differences while diving were more distinct than for surface behaviours. The mean duration of single diving bouts was significantly longer in *N. fodiens* than in *N. anomalus* (U = 9.0, p = 0.003; Table 1). The FR of diving shrews was significantly higher in *N. anomalus* than *N. fodiens* (U = 10.0, p = 0.001). In both species, the FR increased in the following order: floating < swimming < diving (Table 1), and all pairwise intraspecific differences between $FR_{floating}$, $FR_{swimming}$ and FR_{diving} were significant (U = from 0.0 to 25.0 and p = from 0.001 to 0.012).

The total number of dives displayed by 12 individuals of *N. fodiens* was 4 times higher than that displayed by 11 individuals of *N. anomalus* (758 vs 183, Fig. 4; this gives 63.2 vs 16.6 dives/individual, Replicated goodness-of-fit tests: G = 29.02, p < 0.001). The interspecific difference was much higher when the number of difficult dives only (profiles P13, P14, P15, P16) was compared: it was 10 times higher in *N. fodiens* than *N. anomalus* (453 vs 42 difficult dives or 37.8 vs 3.8 difficult dives/individual, $G = 32.24$, $p < 0.001$).

General distribution of frequencies of different types of diving profiles (Fig. 4) did not differ significantly between the two species (Kolmogorov–Smirnov test: $D = 0.188$, $p = 0.895$). However, these distributions were very different from the expected uniform distribution ($D = 0.688$, $p < 0.001$ for *N. anomalus*; $D = 0.875$, $p < 0.001$ for *N. fodiens*), indicating that both species displayed some preferences.

Both species preferred the profiles P10 and P15 (Replicated goodness-of-fit tests: $G = 5.538$ to 40.108, $p < 0.025$ to 0.001); *N. anomalus* preferred additionally P8 ($G = 8.699$, $p < 0.005$) and tended to prefer P2 ($G = 3.544$, $p < 0.1$; Fig. 4). The preferred profiles (P8+P10+P15) constituted 59.0% (73.8% including P2) of all diving profiles performed by *N. anomalus* and 72.3% (P10+P15) in *N. fodiens*. *N. anomalus* performed the easy profile P2 and the medium difficulty profile P8 significantly more frequently than *N. fodiens* ($G = 6.199$, $p < 0.025$ and $G = 9.886$, $p < 0.005$, respectively). In contrast, *N. fodiens* performed the difficult profile P15 much more frequently than *N. anomalus* ($G = 17.276$, $p < 0.001$). While swimming on the bottom, *N. fodiens* stopped and changed the swimming direction much more frequently than *N. anomalus*.

The common profiles avoided by the two species were all shallow and usually long dives P4, P7, P9, P11, and P12 ($G = 4.001$ to 8.664, $p < 0.05$ to 0.005; Fig. 4). Additionally, *N. anomalus* avoided P13 and P16 ($G = 5.619$, $p < 0.025$ in both cases) and *N. fodiens* avoided P1 ($G = 5.683$, $p < 0.025$). The avoided profiles constituted 2.7% and 1.7% of the total diving profiles observed in *N. anomalus* and *N. fodiens*, respectively. *N. anomalus* never performed 3 out of the 16 profiles (P4, P7, P12), whereas *N. fodiens* only one (P12). Moreover, *N. anomalus* avoided three types of difficult profiles (P12, P13, P16), whereas *N. fodiens* only one (P12).

Discussion

Both species spent most of their time in the aquaria swimming on the surface and frequently tried to leave water at the corners of aquaria. Possibly the shrews did not feel comfortable under the experimental conditions (open water surface, no firm ground to rest) and their behaviour could be influenced by stress. These conditions prevented also the shrews from spontaneous swimming and did not give them motives (aquatic prey) for diving. However, the most important fact is that both studied species underwent the same experimental conditions and displayed a list of significant interspecific differences (in 6 out of 10 compared parameters plus differences in diving profiles). And we were interested in these differences rather than whether the behaviour observed in our aquaria mirrored the behaviour of water shrews in the wild. Moreover, in the present study, we were interested only in mechanistic differences in swimming and diving, not in the motives or results of such behaviours. Differences between *N. anomalus* and *N. fodiens* in terrestrial and underwater exploring and foraging (especially the higher success and effectiveness in underwater foraging of *N. fodiens*) under conditions giving shrews many motives, stimuli and opportunity for spontaneous swimming and diving have been already known (Rychlik 1997).

The alternate stroke of the front and hind limbs on a transverse plane was observed in both species. It is considered as an efficient way of swimming (Hickman and Machiné 1986), however, such quadrupedal paddling is less effective than alternate bipedal paddling of hind limbs, typical for most well-adapted semiaquatic mammals (Fish 1993a, b)**.** The swimming velocities of the studied species were not significantly different from one another. This is in contrast to our prediction, since the hind feet (the main propulsive power of water shrews) are longer, the fringes denser and longer, and consequently the paddling surface is larger in *N. fodiens* (Pucek 1981). However, this discrepancy could be readily explained by differences in the stroking frequency of paddling: *N. anomalus*, with a smaller paddling surface, had to stroke more frequently (8.22 str/s vs 7.56 str/s) to reach the same velocity as *N. fodiens*. Unfortunately, we were not able to determine the stroke frequency while diving from our recordings.

The swimming velocities measured in our study (36.4 cm/s in *N. fodiens* and 33.4 cm/s in *N. anomalus*) are slightly lower than those recorded for *N. fodiens* previously (ca. 40 cm/s - Ruthardt and Schröpfer 1985; 36.7-44.1 cm/s - Köhler 1991). This may result from the shorter aquarium used in our experiments (100 cm compared to 300 and 145 cm in the two mentioned papers).

The tail of the two species undulates while swimming on the surface, which is an indication of good swimming skills (Cook et al. 2001). Like in other semi-aquatic mammals, e.g. the muskrat (Fish 1982, 1993b), the tail of water shrews is slightly flattened at the sides due to the keel of stiff hairs on the ventral side (Pucek 1981), and it moves synchronously with the strokes of the hind feet. This is believed to counter-balance the yawing that would be generated by the alternate stroking of the hind limbs, and therefore increases stability during swimming, reduces drag and allows the animals to present a more streamlined frontal view to the water flow (Fish 1982; Kryštufek et al. 2000). *N. fodiens* performed narrower movements with its tail (in relation to its body width) than *N. anomalus*. Apparently, thanks to the longer keel and its greater thrust generation, stable swimming was obtained by *N. fodiens* with a smaller amplitude of tail beats than in *N. anomalus*.

Both water shrew species swam in a similar, almost horizontal mode with their nose near the water surface. Also, both species spent some time floating, with the total duration of this behaviour being somewhat longer in *N. fodiens* than in *N. anomalus*. The mean duration of floating bouts was, however, significantly longer in *N. fodiens* than in *N. anomalus*. This again suggests that *N. fodiens* is better adapted to water than *N. anomalus*. This behaviour has not been described so far for these species. The animals apparently floated while resting or preparing for a dive. Floating, as well as swimming in a horizontal position, can be attributed to high buoyancy (Fish 1993a), which in water shrews results from large amounts of air trapped in their fur (Appelt 1973; Ivanter 1994). Horizontal position and high buoyancy, in turn, can be considered an indication of good swimming skills because paddling forces can be mostly used for propulsion and not wasted in maintaining the head above the water level (Fish 1993a; Cook et al. 2001). This also shows that morphological adaptations, especially those related to the insulating properties of the fur, are very effective and important for the swimming behaviour of water shrews. These adaptations allow the animals to save energy by reduction of heat loss (Vogel 1990; Churchfield 1998) as well as by facilitation of floating and returning to the water surface after diving. However, a high buoyancy also increases the energy costs of paddling downwards and remaining submerged in the water column.

The duration of single dives by *N. fodiens*, registered in different studies, varied from 3 to 16 seconds in laboratory conditions, and from 3 to 24 seconds in the wild (Churchfield 1998; Vogel et al. 1998). In our experiments, *N. fodiens* spent on average 3 seconds and *N. anomalus* 2 seconds under water (with a maximum of 4 and 2.3 seconds, respectively). Although these results can be influenced by size of the aquarium and lack of prey, the most important observation is that the mean duration of diving bouts, as well as the total time spent diving and total number of dives performed, were longer/higher in *N. fodiens* than in *N. anomalus*. These results are consistent with our prediction and, together with interspecific differences in morphological adaptations, may explain why *N. fodiens* forages more efficiently in deep water (Rychlik 1997) and eats more aquatic prey (Churchfield and Rychlik 2006). *N. anomalus* seems to forage by wading in shallow water (Rychlik 1997, 2000; Churchfield and Rychlik 2006) and it may dive to explore the environment or to escape from predators rather than to forage.

The Fineness Ratio (a measure of streamlining - Fish 1993b) of both water shrews increased in the following order: floating < surface swimming < diving, which is logical since the benefit of streamlining increases in the same order. Moreover, compression and loss of air bubbles from the fur during deep diving enhance the streamlining of these species. While swimming and diving, both species had FRs (3.19 to 3.85) within the range of favourable values (3 to 7 - Fish 1993b). Nevertheless, these values were lower than the most optimal FR=4.5 (Fish 1993b). However, such optimal values are observed in aquatic mammals, especially in pursuit-type predators like dolphins and seals (Fish 1993b). Semiaquatic water shrews do not pursue their prey underwater, so their FR can be lower. On the other hand, the fact that during diving *N. anomalus* was flatter (FR=3.85) than *N. fodiens* (3.55) can be explained by different diving modes. *N. fodiens* dived mostly along the bottom (P15) and frequently changed direction, stopped, and shrank or bent its body at the bottom irregularities. In contrast, *N. anomalus* dived more in open water (P2, P8, P10) and its body was usually stretched in straight-line movement. Another cause can lay in a difference in fur quality: possibly less air was retained in the fur of *N. anomalus* than *N. fodiens*.

Both species preferred the deep profiles P10 (of medium difficulty) and P15 (difficult), but *N. fodiens* performed P15 more frequently than *N. anomalus*. *N. anomalus* performed P2 (shallow and easy) and P8 (of medium difficulty) more frequently than *N. fodiens*. Similarly, in the experiment of Haberl (1993), dives to the bottom of aquarium amounted up to 2% in *N. anomalus*, whereas 40% in *N. fodiens*. Generally, in our study the diving profiles performed by *N. fodiens* were more variable and this species avoided (never performed) only one difficult profile. *N. anomalus* never performed three profiles and avoided three difficult ones, indicating that adaptation for diving is lower in this species. However, more detailed experiments utilizing larger tanks (with shallow and deep water compartments and the presence of benthic and pelagic prey) would be useful to further examine the diving abilities of each species. Additional studies examining the physiological attributes (i.e. blood and muscle oxygen carrying capacity and aquatic thermoregulatory abilities) of both species may also prove insightful.

Nevertheless, the results of the present study are very helpful in understanding the field observations: *N. fodiens* prefers sites with direct access to streams and deep water, whereas *N. anomalus* prefers places with shallow water some distance from the stream (Rychlik, 2000). In the wild, aquatic prey compose usually ≥50% of the diet of *N. fodiens* (Churchfield 1984; Kuvikova 1985b) and may reach 95% (Niethammer 1978; DuPasquier and Cantoni 1992). In contrast, the diet of *N. anomalus* may be composed mostly of terrestrial prey (Niethammer 1978; Kuvikova 1987; Churchfield and Rychlik 2006) or only of terrestrial prey (Kuvikova 1985a; Ramalhinho 1995). In laboratory experiments with shallow water (3.5 cm), *N. anomalus* captured many aquatic prey (fish, crustaceans) and utilised them in similar quantities to *N. fodiens* (Rychlik and Jancewicz 2002). However, in experiments with deep water (>10 cm), *N. fodiens* found and took food, whereas *N. anomalus* dived significantly shorter than *N. fodiens* and did not take food placed in such water (Rychlik 1997). Thus, *N. fodiens* is able to forage both in deep and shallow water, while *N. anomalus* can only forage successfully in shallow water (Rychlik 1997, 2000). All these observations are consistent with the results of the present study that demonstrates for the first time qualitatively and quantitatively the differences between *N. fodiens* and *N. anomalus* in swimming and diving abilities. These differences, in turn, may correlate with the different foraging modes used mainly by the two species: wading by *N. anomalus* and diving by *N. fodiens*. Similar differences in swimming and diving abilities have been found in rodents and attributed to the separation of their niches (e.g. Esher et al. 1978; Cook et al. 2001). We can thus conclude that the differentiation in diving abilities and foraging modes may be one of the behavioural mechanisms that allow these two species of water shrews to partition resources and segregate their ecological niches, and in consequence to co-exist syntopically.

Acknowledgments

We are very grateful to R. Schröpfer and A. Schwegmann for access to apparatus and lab, and their help in Osnabrück; to S. Carvalho and M. Simões for their field and technician assistance; to J.R.E. Taylor and G. Ramalhinho for stimulating discussions; and to H. Cabral for help in the statistical analysis. P. Redman kindly improved our English. This study was financed by the Leonardo da Vinci Programme (Agreement no P/03/A/F/PL – 125809), the Polish State Committee for Scientific Research (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

Anonymous (2003) Guidelines for the treatment of animals in behavioural research and teaching. Anim Behav 65:249–255

Appelt H (1973) Fellstrukturuntersuchungen an Wasserspitzmäusen (*Neomys fodiens* (Pennant)). Abh Ber Naturk Mus “Mauritianum” 8:81-87

Biewener AA (2003) Animal locomotion. Oxford University Press, Oxford

Churchfield S (1984) Dietary separation in three species of shrews inhabiting water-cress beds. J Zool 204:211-228

Churchfield S (1998) Habitat use by water shrews, the smallest of amphibious mammals. In: Dunstone N, Gorman ML (eds) Behaviour and ecology of riparian mammals. Cambridge University Press, Cambridge, pp 49-68

Churchfield S, Rychlik L (2006) Diets and coexistence in *Neomys* and *Sorex* shrews in Białowieża Forest, eastern Poland. J Zool 269:381-390

Cook WM, Timm RM, Hyman DE (2001) Swimming ability in three Costa Rican dry forest rodents. Rev Biol Trop 49:1101–1104

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

Esher RJ, Wolfe JL, Layne JN (1978) Swimming behavior of rice rats (*Oryzomys palustri*s) and cotton rats (*Sigmodon hispidu*s). J Mammal 59:551–558

Fish FE (1982) Function of the compressed tail of surface swimming muskrats (*Ondrata zibethicus*). J Mammal 63:591-597

Fish FE (1993a) Comparison of swimming kinematics between terrestrial and semiaquatic opossums. J Mammal 74:275-284

Fish FE (1993b) Influence of hydrodynamic design and propulsive mode on mammalian swimming energetics. Aust J Zool 42:79-101

Haberl W (1993) Zur Ökologie einheimischer Spitzmäuse (Soricidae, Insectivora) und ihres Lebensraumes am Beispiel eines Waldviertler Feuchtbiotops und experimentelle Bearbeitung ausgewählter ethologischer Fragestellungen.) Dissertation, University of Vienna, Vienna, pp 265 + Appendix pp 211

Hickman GC, Machiné C (1986) Swimming behavior in six species of African rodents (Cricetidae, Muridae). Acta Theriol 31:449-466

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

Ivanter EV (1994) The structure and adaptive peculiarities of pelage in soricine shrews. In: Merritt JF, Kirkland GLJr, Rose RK (eds) Advances in the biology of shrews. Special Publication of Carnegie Museum of Natural History No. 18, Pittsburgh, pp 441-454

Köhler D (1991) Notes on the diving behavior of the water shrew, *Neomys fodiens* (Mammalia, Soricidae). Zool Anz 227:218-228

Köhler D (1993) On the learning of the position of underwater food sources by *Neomys fodiens* (Mammalia, Soricidae). Zool Anz 231:73-81

Köhler D (1996) Umwegversuche mit tauchenden Wasserspitzmäusen (*Neomys fodiens*) (Mammalia: Soricidae). Bonn Zool Beitr 46:315-325

Kryštufek B, Davison A, Griffiths HI (2000) Evolutionary biogeography of water shrews (*Neomys* spp.) in the western Palaearctic Region. Can J Zool 78:1616-1625

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

Kuvikova A (1985b) Zur Nahrung der Wasserspitzmaus, *Neomys fodiens* (Pennant, 1771) in der Slowakei. Biológia 40:563-572

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

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

Pucek Z (ed) (1981) Keys to vertebrates of Poland. Mammals. PWN – Polish Scientific Publishers, Warszawa

Ramalhinho MG (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

Ruthardt M, Schröpfer R (1985) Zum Verhalten der Wasserspitzmaus *Neomys fodiens* (Pennant, 1771) unter Wasser. Angew Zool 72(1-2):49-57

Rychlik L (1997) Differences in foraging behavior 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, Suppl 1:173-190

Rychlik L (2004) Competition and coexistence of shrews. In: Jędrzejewska B, Wójcik JM (eds) Essays on mammals of Białowieża Forest. Mammal Research Institute, Polish Academy of Sciences, Białowieża, pp 161-170

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

Rychlik L, Zwolak R (2005) Behavioural mechanisms of conflict avoidance among shrews. Acta Theriol 50:289-308

Rychlik L, Zwolak R (2006) Interspecific behavioural domination among four sympatric species of shrews. Can J Zool 84:434-448

Sokal RR, Rohlf FJ (1995) Biometry. The principles and practice of statistics in biological research. WH Freeman and Company, New York

Spitzenberger F (1990) Gattung *Neomys* Kaup, 1829. In: Niethammer J, Kapp F (eds) Handbuch der Säugetiere Europas. Band 3/1. Insektenfresser, Herrentiere. Aula-Verlag, Wiesbaden, pp 317-333

Spitzenberger F (1999) *Neomys anomalus* Cabrera, 1907. *Neomys fodiens* (Pennant, 771). In: Mitchell-Jones AJ, Amori G, Bogdanowicz W, Kryštufek B, Reijinders PJH, Spitzenberger F, Stubbe M, Thissen JB, Vohralik V, Zima J (eds) The atlas of European mammals. T and AD Poyser Ltd, London, pp 58-61

Torre I, Tella JL (1994) Distribution of the Cabrera water shrew (*Neomys anomalus*) in northeastern Spain. Z Säugetierk 59:282-288

Vogel P (1990) Body temperature and fur quality in swimming water-shrews *Neomys fodiens* (Mammalia: Insectivora). Z Säugetierk 50:73-80

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

Table 1. Summary of differences between *Neomys anomalus* and *N. fodiens* in surface swimming, floating and diving. Significance of the differences (revealed by Mann-Whitney *U*-test): ns – insignificant, ** $p \leq 0.01$, *** $p \leq 0.005$, **** $p \leq 0.001$. The sample size n varies because particular parameters were not displayed by or measurable in all tested animals.

Parameter of behaviour	*N. anomalus*		Difference	*N. fodiens*		Significance of difference
	mean ± SD	n		mean ± SD	n	
			Swimming			
Velocity (cm/s)	33.36 ± 1.35	9	=	36.44 ± 2.34	9	ns
Stroking frequency (str./s)	8.22 ± 0.47	10	>	7.56 ± 0.61	11	**
Inclination (°)	12.02 ± 2.25	11	=	12.64 ± 1.09	9	ns
Body width : tail width ratio	1.09 ± 0.04	8	<	1.13 ± 0.06	7	***
Body width : body length ratio	0.36 ± 0.01	8	<	0.39 ± 0.01	7	***
Fineness Ratio	3.19 ± 0.339	11	=	3.26 ± 0.310	11	ns
			Floating			
Duration of single bout (s)	1.28 ± 0.32	9	<	2.00 ± 0.74	9	**
Fineness Ratio	2.02 ± 0.178	5	=	2.05 ± 0.197	6	ns
			Diving			
Duration of single bout (s)	2.12 ± 0.55	9	<	3.08 ± 0.56	9	***
Fineness Ratio	3.85 ± 0.17	10	>	3.55 ± 0.16	12	****

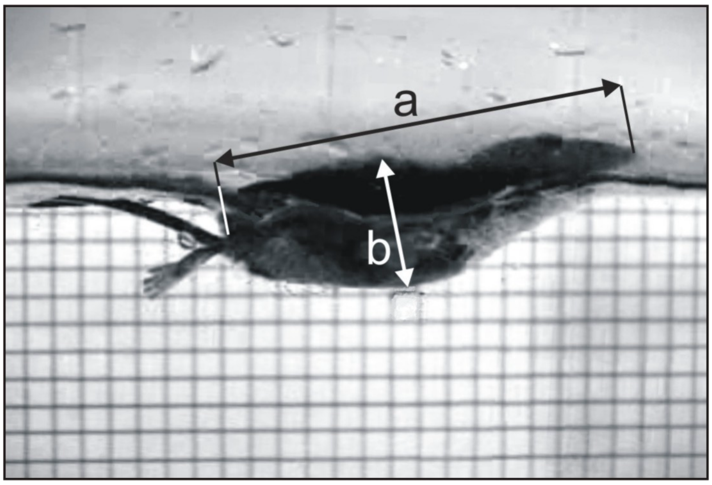

Fig. 1. *Neomys fodiens* swimming at the water surface. Measurements for the Fineness Ratio calculation (FR = a/b) and the position of nose are visible.

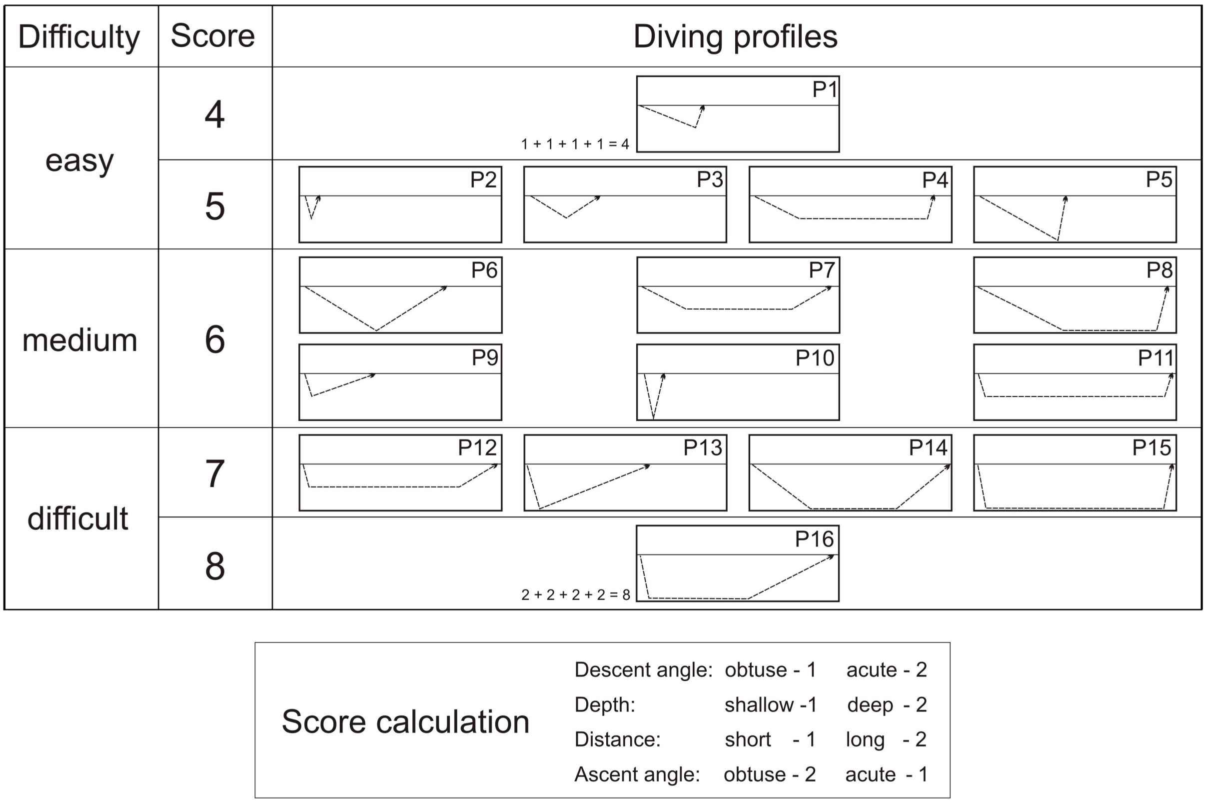

Fig. 2. Sixteen diving profiles distinguished in this study and ordered according to their difficulty (scores from 4 to 8).

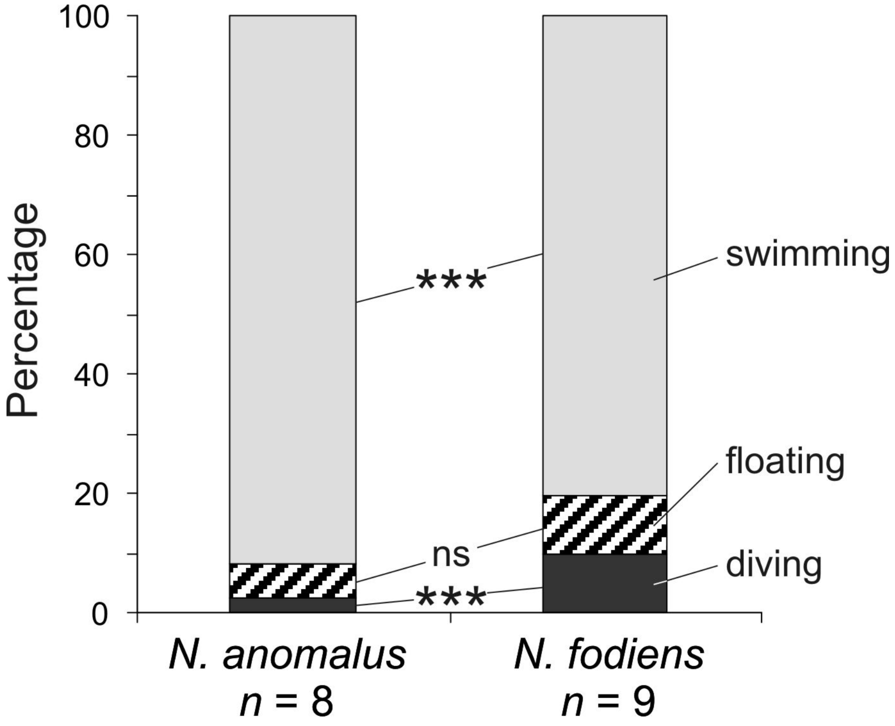

Fig. 3. Proportions of floating, swimming and diving displayed by the two species of *Neomys* during the total time of a test. 100% = 5 minutes, *n* – number of water shrews that displayed all three kinds of behaviour. Significance of the differences (revealed by Mann-Whitney *U*-test): ns – insignificant, *** $p \leq 0.005$.

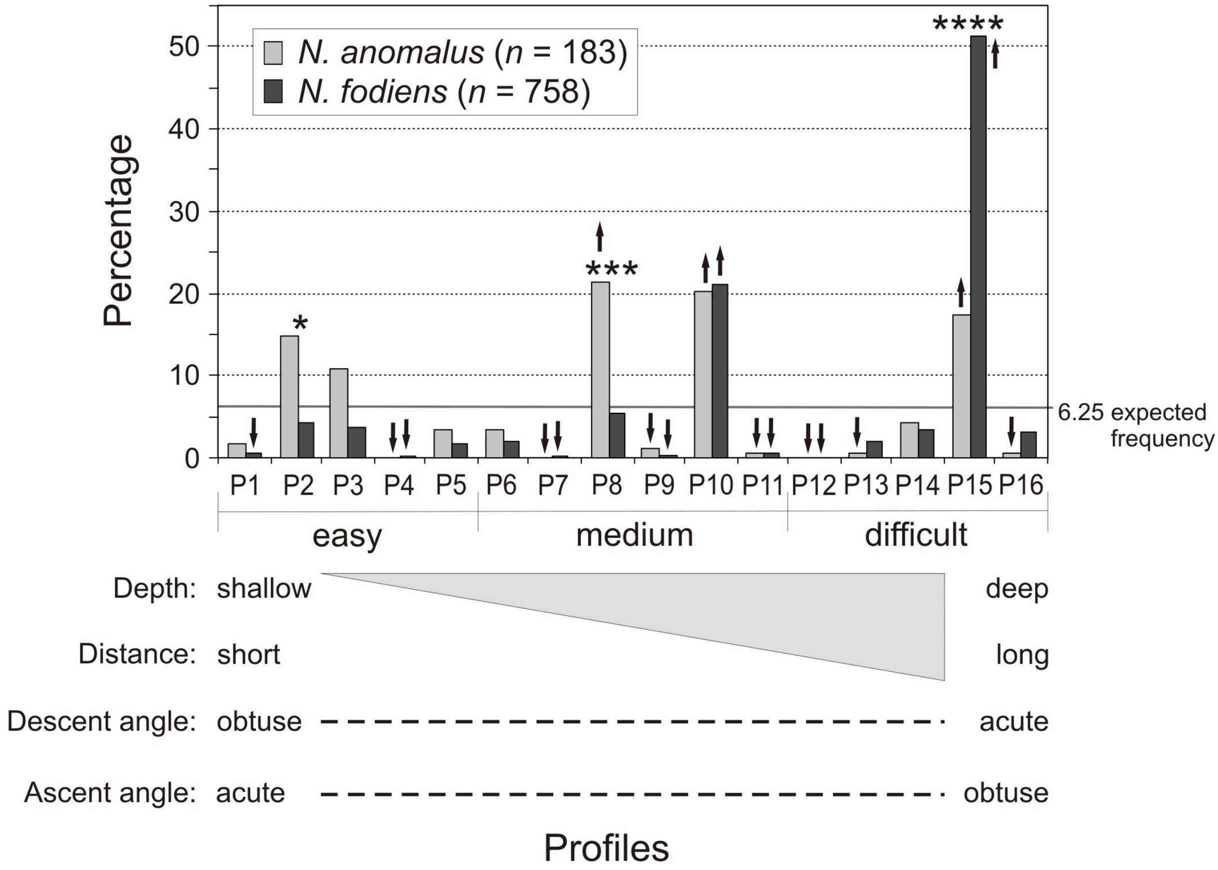

Fig. 4. Differences in diving profiles between *Neomys anomalus* and *N. fodiens*. Significance (revealed by goodness-of-fit *G*-test) of interspecific differences: * $p \leq 0.05$, *** $p \leq 0.005$, **** $p \leq 0.001$; differences between expected and observed values: arrow up - preferred profile (significantly more frequent than expected), arrow down - avoided profile (significantly less frequent than expected).