Interspecific aggression and behavioural dominance among four sympatric species of shrews

Leszek Rychlik and Rafal Zwolak

Abstract: Level of interspecific aggression should reflect intensity of interference competition, and large dominant and small subordinate species should develop aggressive and passive agonistic behaviours, respectively, to achieve stable coexistence. We tested these ideas, investigating interspecific behavioural dominance in a four-species community of shrews varying in body size (*Sorex minutus* L., 1766; *Sorex araneus* L., 1758; *Neomys anomalus* Cabrera, 1907; *Neomys fodiens* (Pennant, 1771)) by placing interspecific pairs in a neutral field. The order of dominance (determined on the basis of duration of offensive and defensive behaviours, total time spent in the shelter, and a "final shelter resident" index) corresponded to the order of body size: *N. fodiens* > *N. anomalus* > *S. araneus* > *S. minutus*. The highest number of conflicts and the least pronounced dominance of *N. anomalus* over *S. araneus* suggest that the interference competition was strongest between these species. The different social organization of *N. anomalus* (tolerant and gregarious versus intolerant and solitary in the other three species) did not decrease its aggressiveness and dominance rank. The larger *Neomys* species were more aggressive and initiated relatively more offensive behaviours, whereas the smaller *Sorex* species initiated more defensive behaviours. The presence of food and shelter did not intensify conflicts. Nevertheless, dominant species restricted the access of subordinate species to the shelter.

Résumé : Le niveau d'agressivité interspécifique devrait refléter l'intensité de la compétition d'interférence; les espèces dominantes de grande taille et les espèces subordonnées de petite taille doivent développer des comportements agonistes respectivement agressifs et passifs afin d'établir une coexistence stable. Nous avons testé ces idées en étudiant la dominance comportementale interspécifique dans une communauté de quatre espèces de musaraignes qui diffèrent par leur taille (*Sorex minutus* L., 1766; *Sorex araneus* L., 1758; *Neomys anomalus* Cabrera, 1907; *Neomys fodiens* (Pennant, 1771)), en les plaçant par paires interspécifiques dans un champ neutre. L'ordre de dominance (d'après la durée des comportements offensifs et défensifs, le temps total passé dans le refuge et l'indice du « résidant final du refuge ») correspond à l'ordre des tailles, soit *N. fodiens* > *N. anomalus* > *S. araneus* > *S. minutus*. Le nombre maximal de conflits et la dominance la moins marquée chez *N. anomalus* par rapport à *S. araneus* indiquent que la compétition d'interférence la plus forte existe entre ces deux espèces. L'organisation sociale différente de *N. anomalus* (tolérante et grégaire au lieu d'intolérante et solitaire, comme les trois autres espèces) ne diminue pas son agressivité et son rang de dominance. Les *Neomys,* de plus grande taille, sont plus agressifs et initient relativement plus de comportements offensifs, alors que les *Sorex,* de plus petite taille, initient plus de comportements défensifs. La présence de nourriture et d'un refuge n'intensifie pas les conflits. Néanmoins, les espèces dominantes restreignent l'accès des espèces subordonnées au refuge.

[Traduit par la Rédaction]

Introduction

Interspecific competition is one of the main mechanisms shaping communities of animals (e.g., Pianka 1981; Connell 1983; Schoener 1983; Tilman 1987; Keddy 1989), including small mammals (for reviews see Grant 1972, 1976; Dickman 1991; Kirkland 1991; Fox and Kirkland 1992; Eccard and Ylönen 2003). It is considered particularly important in regulating the structure of guilds (May 1981; Camargo 1992), i.e., groups of species that exploit the same type of resources in similar ways (Root 1967). So far, most research on competition in small mammals has concerned rodents and has focused on the influence of exploitation competition on microhabitat selection or population dynamics (Eccard and Ylönen 2002, 2003). There are far fewer studies on interference competition (Eccard and Ylönen 2002) and, in general, much less is known about competition among shrews (Kirkland 1991).

Interference competition occurs when some individuals directly (e.g., by fighting) reduce the access of other individ-

Received 29 July 2005. Accepted 30 January 2006. Published on the NRC Research Press Web site at http://cjz.nrc.ca on 18 March 2006.

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doi:10.1139/Z06-017

uals to a limited resource (Feldhamer et al. 1999). Aggression seems to be primarily an adaptation to cope with competition (Moynihan 1998), so the amount of agonistic behaviour directed towards a competitor should reflect the degree of true competition (MacArthur 1977). Experiments performed on different animals demonstrated direct aggression contributing to interspecific competition (e.g., Grant 1970, 1972; Frye 1983; Downes and Bauwens 2002; Langkilde and Shine 2004) as well as interspecific tolerance and noncompetitive coexistence (e.g., Wolff and Dueser 1986; Perri and Randall 1999). Usually, (*i*) the level of aggression is higher between sympatric and closely related species than between allopatric and unrelated ones (Nevo et al. 1975; Dempster and Perrin 1990), (*ii*) ecological “specialist” species dominate “generalists” (Blaustein and Risser 1976; Ambrose and Meehan 1977; Dempster and Perrin 1990), and (*iii*) larger species dominate smaller species (Ambrose and Meehan 1977; Frye 1983; Schoener 1983; Johannesen et al. 2002; Langkilde and Shine 2004). However, dominance of smaller species over larger ones has also been observed (e.g., Miller Baker 1974; Dempster and Perrin 1990).

Since interspecific interference competition is often asymmetric, dominant and subordinate species may optimize their behaviour in different ways (Maynard Smith and Parker 1976; Law et al. 1997). According to the theory (Persson 1985; Young 2003), large dominant species should develop active aggression (e.g., attacks, chases, offensive threats), whereas small subordinate species should develop rather passive agonistic behaviours (e.g., avoidance, escape, freezing, defensive postures and vocalizations). Interspecific aggression, dominance, and territoriality are advantageous because they reduce competition for resources and risk of injury, and save time and energy (Oksanen et al. 1979; Kaufmann 1983; Moynihan 1998). They function also as mechanisms keeping sympatric species ecologically separate (Blaustein and Risser 1976), and thus facilitate their stable coexistence.

Soricine shrews seem to be an excellent model to use to investigate competition because (*i*) they usually coexist in multispecies communities (Kirkland 1991; e.g., nine species in central Siberia, Churchfield and Sheftel 1994); (*ii*) their metabolic rates and food requirements are the highest among mammals (McNab 1991; Taylor 1998); (*iii*) they are intra- and inter-specifically aggressive, intolerant, and territorial (Rychlik 1998); (*iv*) they are very sensitive to changes in different biotic and abiotic factors such as prey availability, population density, temperature, and humidity (Churchfield 1990; Hanski 1994; Gliwicz and Taylor 2002). All this requires from them particularly effective mechanisms of resource partitioning. An advantage of the small body size of shrews is that more species can coexist in a given habitat (Kirkland 1991). However, a relatively large body size confers a competitive advantage on the members of a shrew community, because it facilitates access to higher quality foraging microhabitats (Fox and Kirkland 1992).

Four species of soricine shrews coexist in the wet habitats of Białowieża Forest (eastern Poland): Eurasian pygmy shrew, *Sorex minutus* L., 1766, Eurasian common shrew, *Sorex araneus* L., 1758, Mediterranean (southern) water shrew, *Neomys anomalus* Cabrera, 1907, and Eurasian water shrew, *Neomys fodiens* (Pennant, 1771). They form a guild (Schröpfer 1990), so intra- and inter-specific competition for resources can be expected. Previous studies on niche segregation among these species included foraging modes (Rychlik 1997), food preferences and handling (Rychlik and Jancewicz 1998, 2002), diets (Churchfield and Rychlik 2006), microhabitat preferences (Rychlik 2000, 2001), circadian activity (Rychlik 2005), and avoidance of aggression (Zwolak and Rychlik 2004; Rychlik and Zwolak 2005). Considerable interspecific overlaps in different niche dimensions were observed. The species display several forms of conflict avoidance (Rychlik and Zwolak 2005), but a clear hierarchy of behavioural dominance can act as another mechanism ensuring their stable coexistence.

In this paper we examine another aspect of the current sympatry of these species of shrews: aggressiveness and dominance in interspecific behavioural interactions. Because the above-mentioned species vary in body size, we expected that this factor would strongly influence the pattern of interspecific dominance. Furthermore, we gave particular attention to the dominance rank of *N. anomalus*, as this rare species has been poorly investigated. Moreover, in contrast to the vast majority of soricine shrews, which are strictly territorial and solitary, *N. anomalus* shows considerable intraspecific tolerance and is supposedly more gregarious (Krushinska and Rychlik 1993; Krushinska et al. 1994; Rychlik 1998). Thus, one may expect that *N. anomalus* will differ from the other studied species in the level of aggressive behaviour. Previous studies (Krushinska and Pucek 1989; Krushinska and Rychlik 1993; Krushinska et al. 1994) showed that both species of water shrews engaged in many conflicts near food and, especially, shelter. Thus, we also attempted to determine whether competition for food or shelter changed the level of aggression and the dominance order among the tested species.

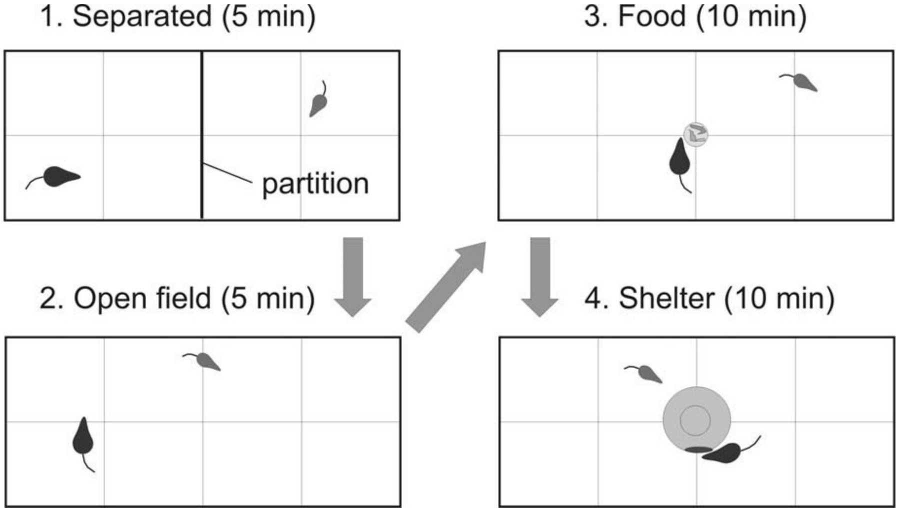
We formulated five hypotheses concerning factors that may affect aggressiveness and interspecific dominance rank: (1) the dominance rank of a species is positively correlated with its body size; (2) dominant and subordinate species display different kinds or proportions of agonistic behaviours; (3) aggressiveness and dominance rank of a given species are influenced by its social organization; (4) competition for resources (such as food or shelter) increases intra- and interspecific aggressiveness; and (5) dominant species restrict the access of subordinate species to resources. In consequence, we tested the following predictions: (*i*) the level of aggression and dominance rank will be the higher in larger species of shrews; (*ii*) large dominant and small subordinate species will display mainly aggressive and passive agonistic behaviours, respectively; (*iii*) the level of aggression and dominance rank of the gregarious *N. anomalus* will be lower than expected according to its body size; (*iv*) the presence of food or shelter will increase intra- and inter-specific aggressiveness and conflicts; and (*v*) dominant species of shrews will spend more time near food and in shelter than subordinate species of shrews.

Methods

Catching and maintaining the animals

Wild shrews were captured in wet habitats of Białowieża Forest between June and September of 2000–2002. Pitfall traps containing a handful of moss as bedding and a tea-

Fig. 1. Experimental design, showing conditions and durations of the four stages of tests.



spoon of minced beef as bait/food and covered with a roof for protection from rain were used for live-trapping. The traps were opened in the afternoon (usually about 1700), checked every 2–2.5 h, and closed usually about midnight. Trapping was not performed during heavy rainfall and cold evenings. Animals were transported to the laboratory in buckets containing moss bedding and food (minced beef and fly larvae). Transportation lasted 10–20 min. In the laboratory shrews were placed in individual cages (30 cm × 40 cm × 15 cm), where they were acclimatized to conditions of captivity for at least 5 days. The cages were equipped with a shelter (an inverted pot filled with moss) and litter (a mixture of sand, sawdust, peat, and moss). Food (minced meat, fly larvae, mealworms, and dried *Gammarus* sp.) and water were provided ad libitum. In the laboratory, a natural cycle of light and darkness was maintained, temperatures oscillated between 16 and 20 °C, and air humidity was about 80%. The tested shrews spent 1–8 weeks in captivity, but most were kept for ca. 3 weeks and only nine were kept for longer than 4 weeks.

Testing procedure

Because of the shrews' cryptic life style, it was not possible to study their aggressive interactions in the field. For this reason we adopted the laboratory method of dyadic encounters in a neutral arena. This method has been frequently used to investigate interspecific interactions among rodents (e.g., Dempster and Perrin 1990; Cihakova and Frynta 1996; Harper and Batzli 1997; Johannesen et al. 2002). It was also employed to investigate different aspects of the intraspecific social behaviour of shrews (e.g., Moraleva 1989; Baxter and Irwin 1995; Shchipanov et al. 1998; Oleinichenko 2000), but studies on their interspecific interactions in a neutral arena remain scarce (e.g., Krushinska and Pucek 1989; Kalinin et al. 1998).

A total of 69 subadult individuals (i.e., young of the year, fully grown but sexually immature) were used in dyadic encounters: 17 *S. minutus*, 19 *S. araneus*, 15 *N. anomalus*, and 18 *N. fodiens*. The possibility that some of these shrews were siblings cannot be excluded, but because the animals were captured in several different sites and over a few successive years, such instances were probably rare. It was impossible to sex these animals and test one-sex dyads, but the social behaviour of subadult males and females is similar (Rychlik 1998). Animals were tested in a separate room during daytime, usually between 0900 and 1600, i.e., during the period when the activity of shrews decreases to some extent (Rychlik 2005). To ensure that the tested animals were not satiated, feeding trays were removed from their cages approximately 1 h before the experiment began. A pair of animals was placed in a neutral arena, i.e., a bare glass terrarium measuring 70 cm × 30 cm × 40 cm (Fig. 1), and their behaviour was video-recorded. A Sony SSC-C370P camera, Panasonic NV-FS100HQ video recorder (VHS system), and Sony KV-X2531B monitor were used. To ensure an adequate record, the terrarium was illuminated with a 60 W lamp suspended about 1.5 m above it. After each test the terrarium was carefully washed with detergent.

Each test lasted 30 min and consisted of four consecutive parts. In the first part (separated, 5 min) the animals stayed in different halves of the terrarium, separated by a transparent plastic partition (Fig. 1). During this stage, the shrews could settle in after their removal from individual cages and explore their new surroundings without physical contact with the second individual. A similar period (3–5 min) was used in other studies (e.g., Cranford and Derting 1983; Krushinska and Pucek 1989; Dempster and Perrin 1990; Harper and Batzli 1997). In the second part (open field, 5 min), the partition was removed and the animals could begin to interact in a neutral open field. In the third part (food, 10 min) a bowl containing minced meat was placed in the terrarium to elicit competition for food. In the fourth stage (shelter, 10 min) the bowl was replaced with an inverted pot that served as a shelter (Fig. 1). Since most soricine shrews are unable to utilize resources communally (Rychlik 1998), the introduction of only one bowl and one shelter ensured that resources were in short supply. Previously, Krushinska and Pucek (1989) placed two water shrews for 5 min in separate halves of an arena and then tested them for 30 min in the open field and then for another 30 min after the shelter was introduced (65 min in total). To avoid prolonged aggressive encounters, we shortened the duration of our tests to 30 min. For com-

Table 1. The numbers of tests carried out on particular combinations of four shrew species.

	Sorex minutus	*Sorex araneus*	*Neomys anomalus*
Sorex araneus	12 (11/12*)	—	—
Neomys anomalus	9 (9/8[†])	10 (10)	—
Neomys fodiens	10 (10)	10 (10)	9 (9)

Note: Numbers in parentheses show the number of results obtained.
*Eleven results for *S. minutus* and 12 for *S. araneus*.
[†]Nine results for *S. minutus* and eight for *N. anomalus*.

parison, in recent studies, agonistic interactions among shrews have usually been tested in an open field for 10–12 min (Baxter and Irwin 1995; Kalinin et al. 1998; Shchipanov et al. 1998; Oleinichenko 2000).

Immediately after the trials, animals were weighed with an accuracy of 0.1 g and placed back in their individual cages. Mean body masses were as follows: 2.83 g for *S. minutus* (range 2.2–4.3 g, $n = 38$ measurements), 7.42 for *S. araneus* (range 6.3–8.7 g, $n = 42$), 9.75 for *N. anomalus* (range 7.9–12.7 g, $n = 40$), and 14.40 for *N. fodiens* (range 10.4–18.0 g, $n = 40$).

A total of 60 interspecific trials were conducted and the number of tests per pair of species is presented in Table 1. It was not possible to capture enough shrews to use each only once, so each individual took part in one to four (usually two) tests, each time with a different species (in random order). The only exceptions were that one *N. anomalus* participated in two tests with *S. minutus* and one *S. minutus* in two tests with *S. araneus*. In both cases we took into account only the first of the two trials in describing the behaviour of *N. anomalus* and *S. minutus*, and used the second trial only to describe the behaviour of the opponent (see Table 1). Consecutive tests of the same individual were separated by at least a 3 day break, which apparently reduced the carry-over effect of loss or victory in a prior trial.

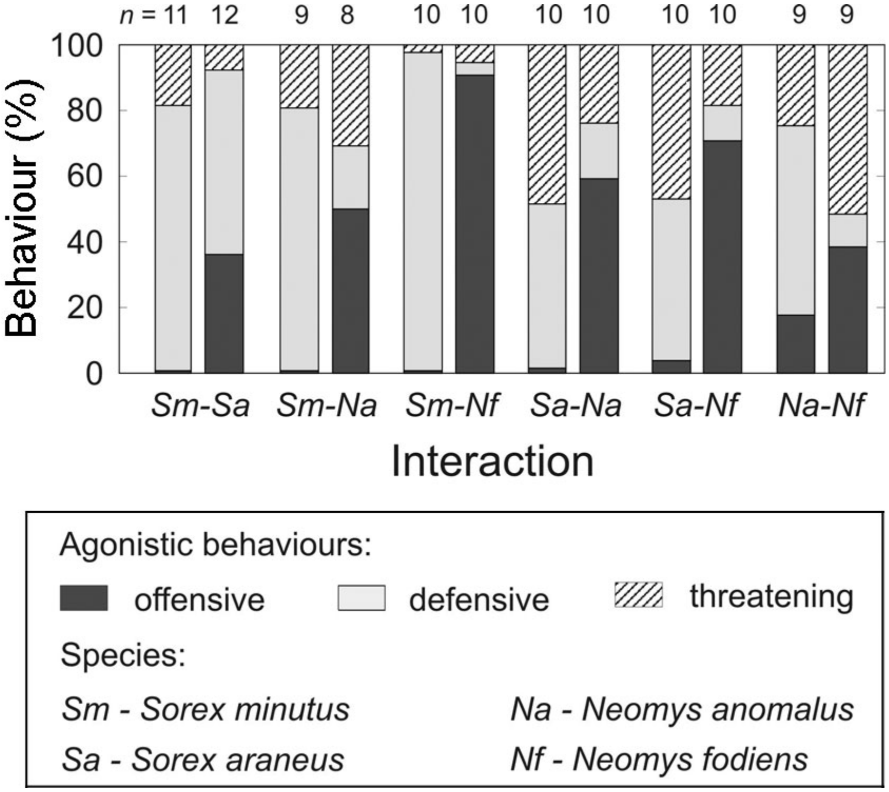
The social behaviour of shrews was previously analyzed and categorized by several authors (Olsen 1969; Martin 1980; Baxter and Irwin 1995; Shchipanov et al. 1998). To obtain data comparable to the existing results, following the above-mentioned authors we classified the observed behaviour of shrews as follows. (1) Non-agonistic — this is divided into (*i*) amicable (or integrative): "naso-anal whirling" (intensive reciprocal sniffing, when two shrews remained in close contact, almost intertwined), crawling on each other, and moving around; (*ii*) neutral (or identification): approaching the other animal and sniffing it from some distance away; (*iii*) contact avoidance (or rejection): "keeping-distance behaviour" (avoiding the adversary by means of simultaneous movements at a more or less constant distance), "to-and-fro behaviour" (approaching the other animal, followed by quick withdrawal), and "freeze" (motionless except for the vibrissae and snout); (*iv*) marking: dragging the anogenital area against the terrarium floor. (2) Agonistic — this is divided into (*i*) offensive behaviours: rush (without contact/bite), attack (with contact/bite), hopping towards (without contact/bite), jumping on (with contact/bite), combat (both head to head and head to tail), chase (quick, at a short distance), and follow (slower, at some distance); (*ii*) defensive behaviours: retreating, jumping away, and escaping (i.e., running away), all as a result of direct contact; (*iii*) threats: stance, tripedal, sideways, back, and upright postures, and threatening vocalization (this occurred during almost every conflict, regardless of whether the animals fought or stopped at threats). Vocalizations were not analyzed because identification of the vocalizing individual in an interacting pair was unreliable. (3) Resource use — this is divided into (*i*) food utilization: eating and sniffing food, remaining in tactile contact with a bowl containing food; (*ii*) shelter occupation: staying inside the shelter or protruding from its entrance. (4) Other (not analyzed in the present paper) — this includes exploration (walking, running, sniffing, jumping onto the terrarium walls or nest box, attempting to dig), attentive behaviour (active but remaining in place), resting, self-grooming, and defecation/urination.

Determination of dominance hierarchy

Behavioural dominance and subordination are defined here not in terms of the social rank of individuals within a group of conspecifics, but as the position of a species in competitive interactions within a community of species. We assumed that by averaging the results of interactions between individuals of different species we would be able to determine dominance of one species over another. We compared mean total times spent displaying offensive and defensive behaviours by particular shrew species over a 5 min period. These behaviours occurred usually in long (often consecutive) bouts, which could not be divided into single acts. Therefore, we used the total duration (not the mean number) of acts per unit of time. As in many previous studies (Blaustein and Risser 1976; Cranford and Derting 1983; Kaufmann 1983; Krushinska and Pucek 1989; Dempster and Perrin 1990; Lehner 1998), we accepted that a species that attacked more often and escaped less often was dominant in a given interaction. Additional measures of dominance were total time spent near food, total time spent in the shelter, and presence in the shelter during the last minute of the test. We assumed that dominant shrews would spend more time near food and in the shelter, and would be the last occupants of the shelter.

Threatening occurred in the context of both offense and defense, hence we did not regard this behaviour as a direct measure of dominance. Nevertheless, we assumed that a high level of threatening would indicate intensive conflicts and suggest their equivocal outcome (i.e., the more threats that are made during interactions between the animals/species in a given pair, the less definitive the dominance of one individual/species over the other). To investigate the effects of competition for resources on dominance hierarchy, we compared the durations of offensive and defensive behaviours in consecutive stages of the trials (open field, food, and shelter).

Fig. 2. Percentages of the different kinds of agonistic behaviours displayed by shrews during interspecific interactions over 5 min in the open-field test stage. Each bar illustrates the behaviours initiated reciprocally by each of the two opponents; for example, in the "Sm–Sa" combination, the bar on the left side represents the durations of behaviours initiated by *Sorex minutus* towards *Sorex araneus* and the bar on the right side shows the durations of behaviours initiated by *S. araneus* towards *S. minutus* (*n* is the sample size; cf. Methods and Table 1).



Data analysis

The duration of a single behavioural act was measured with an accuracy of 1 s. The durations of particular categories of behaviour were summed separately for each stage of the test and expressed as the total duration per 5 min. The results of all trials for a given pair of species were averaged and these means are presented as graphs, along with standard errors. The mean durations of agonistic behaviours (offensive + defensive + threatening) were converted to percentages (their sums being 100%) and are presented in Fig. 2. In most statistical analyses, three steps were performed: (1) Comprehensive Kruskal–Wallis tests were calculated to estimate diversification within each group of compared results. (2) For significantly diversified groups, post-hoc two-sample tests were performed; intraspecific differences were compared using Wilcoxon tests, whereas interspecific or intercombination differences were tested using Mann–Whitney *U* tests and replicated goodness-of-fit tests (*G* statistic) (Sokal and Rohlf 1995). (3) Since these multiple comparisons could increase the chance of Type 1 error, the conventional level of significance ($p < 0.05$) was adjusted by applying the "false discovery rate" (FDR) procedure (Curran-Everett 2000), which has some advantages over the commonly used Bonferroni and other procedures. The following computer programs were used: Observer Video-Pro® version 4.1, FoxPro® version 2.5b, MS Excel® 97, GraphPAD InStat® version 1.13, and SYSTAT® version 5.03.

Ethical note

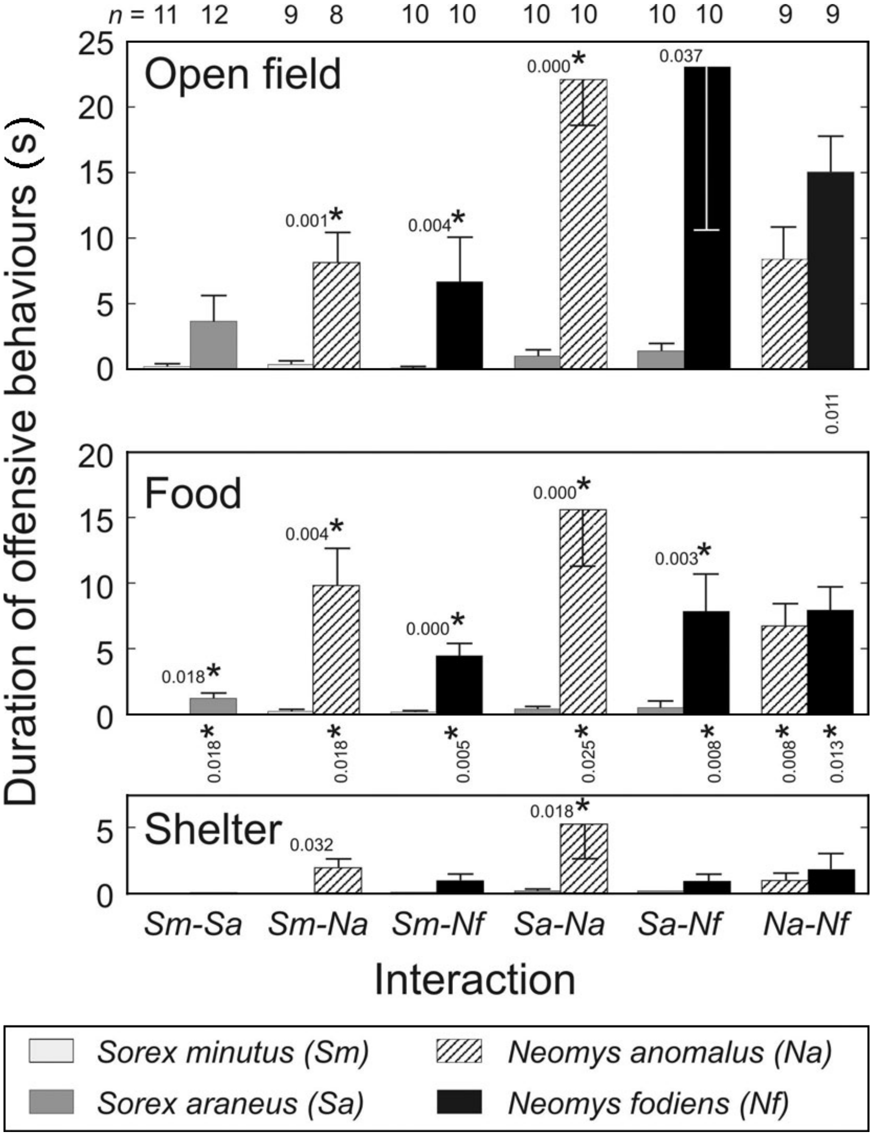
The animals were cared for in accordance with *Guidelines for the treatment of animals in behavioural research and teaching* (Anonymous 2003). Pregnant and lactating females were caught only sporadically. They (as well as adult males and other unwanted small mammals) were immediately released at the place of capture. We planned to stop all conflicts that posed a threat to the health of the animals. However, we did not have to interrupt any tests. None of the animals died during or directly after a trial. After the study, 36 animals were used in other laboratory investigations, while 33 were released back in the wild. We obtained permission (DLOPiKog. 4201-206/00 of 17 July 2000 and DLOPiKog. 4201-04-136/2001/2002 of 28 February 2002) from the Minister of Environment for capturing the protected shrews and acceptance (2001/11 of 11 January 2001) from the Local Ethical Commission for Experiments with Animals in Białystok (Poland) for our experimental methods.

Results

Interspecific differences in agonistic behaviour

Sorex minutus initiated a lot of defensive interactions (significantly more than its three opponents: G = 4.561–105.580, $p < 0.05$ and $p < 0.001$; Fig. 2). The proportion of threats displayed by *S. minutus* towards *N. fodiens* was significantly lower than towards *S. araneus* and *N. anomalus* (G = 13.161 and 14.287, respectively, $p < 0.001$). *Sorex*

Fig. 3. Total durations (mean ± SE) of offensive behaviours displayed by shrews per 5 min during the three test stages (open field, food, and shelter). Values at $p \leq 0.05$ for differences between pairs of compared species (revealed by Mann–Whitney *U* tests) are shown above the bars within the panels; values at $p \leq 0.05$ for intraspecific differences between the consecutive test stages (revealed by Wilcoxon tests) are shown between the panels. An asterisk indicates a significant difference after the levels of significance in both tests are adjusted using the “false discovery rate” procedure. See Fig. 2 for further details.



araneus displayed significantly more threats and fewer offensive behaviours towards *N. anomalus* and *N. fodiens* than towards *S. minutus* (threats: $G = 32.313$ and 31.231, respectively, $p < 0.001$; attacks: $G = 39.782$ and 31.474, respectively, $p < 0.001$). *Neomys anomalus* displayed significantly more offensive behaviours towards the two *Sorex* species than towards *N. fodiens* (*N. anomalus* towards *S. minutus* vs. *N. anomalus* towards *N. fodiens*, $G = 15.903$, $p < 0.001$; *N. anomalus* towards *S. araneus* vs. *N. anomalus* towards *N. fodiens*, $G = 23.344$, $p < 0.001$), whereas the opposite occurred with defensive behaviours ($G = 19.954$, $p < 0.001$, and $G = 23.817$, $p < 0.001$, respectively). The stronger the opponent, the shorter the offensive behaviours and the longer the threats displayed by *N. fodiens*; the proportion of offensive behaviours decreased from 90.5% in interactions with *S. minutus* through 70.4% with *S. araneus* to 38.7% in interactions with *N. anomalus*, whereas the proportion of threats increased from 5.4% in interactions with *S. minutus* through 18.3% with *S. araneus* to 51.7% in interactions with *N. anomalies*.

Behavioural dominance

The duration of offensive behaviours (Fig. 3) was very diversified among species combinations in all three stages of the tests (Kruskal–Wallis test, $H = 33.242–82.684$, $p = 0.000$, df = 11). In each combination of species and all stages of the tests, individuals of larger species attacked longer and more frequently. After the FDR procedure, the differences were significant in three out of six interspecific combinations in the open-field stage (Mann–Whitney *U* test, $U = 2.0–11.5$, $p = 0.001–0.037$), five combinations in the food stage ($U = 1.0–27.5$, $p = 0.0003–0.018$), and one com-

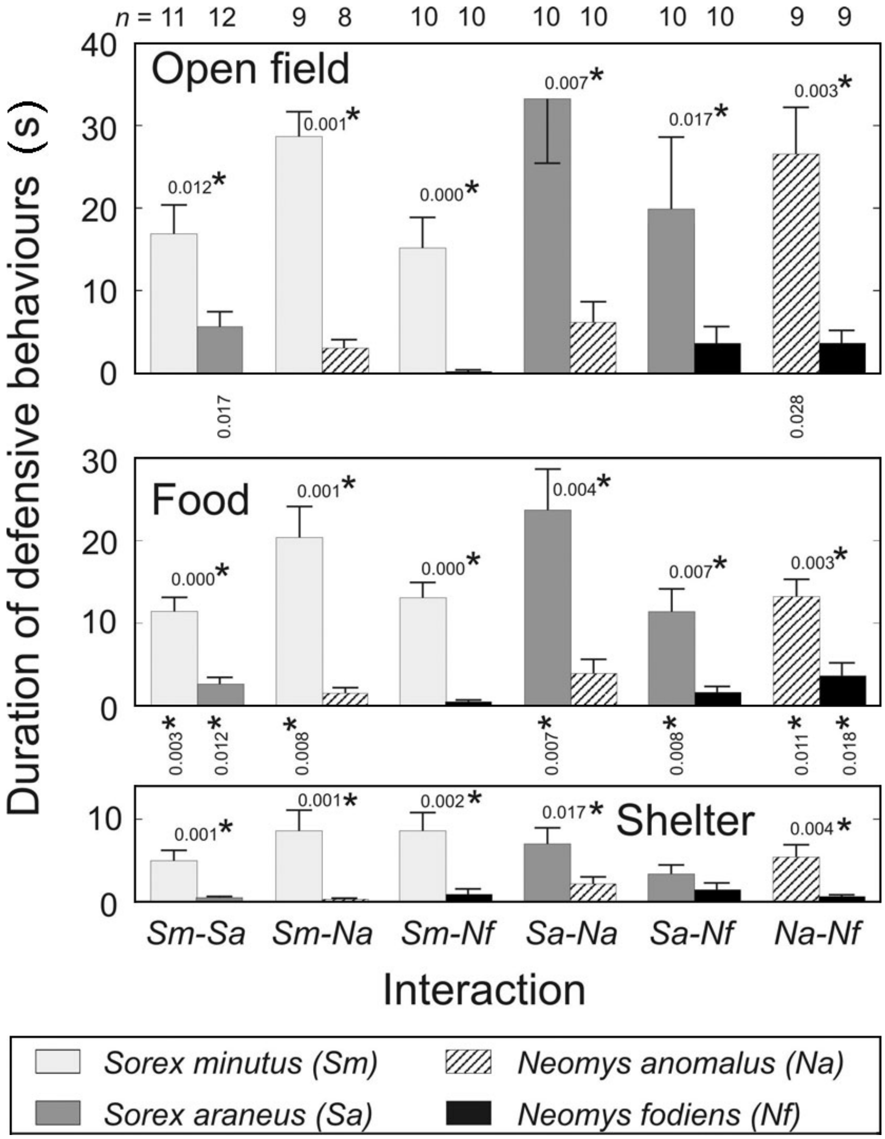


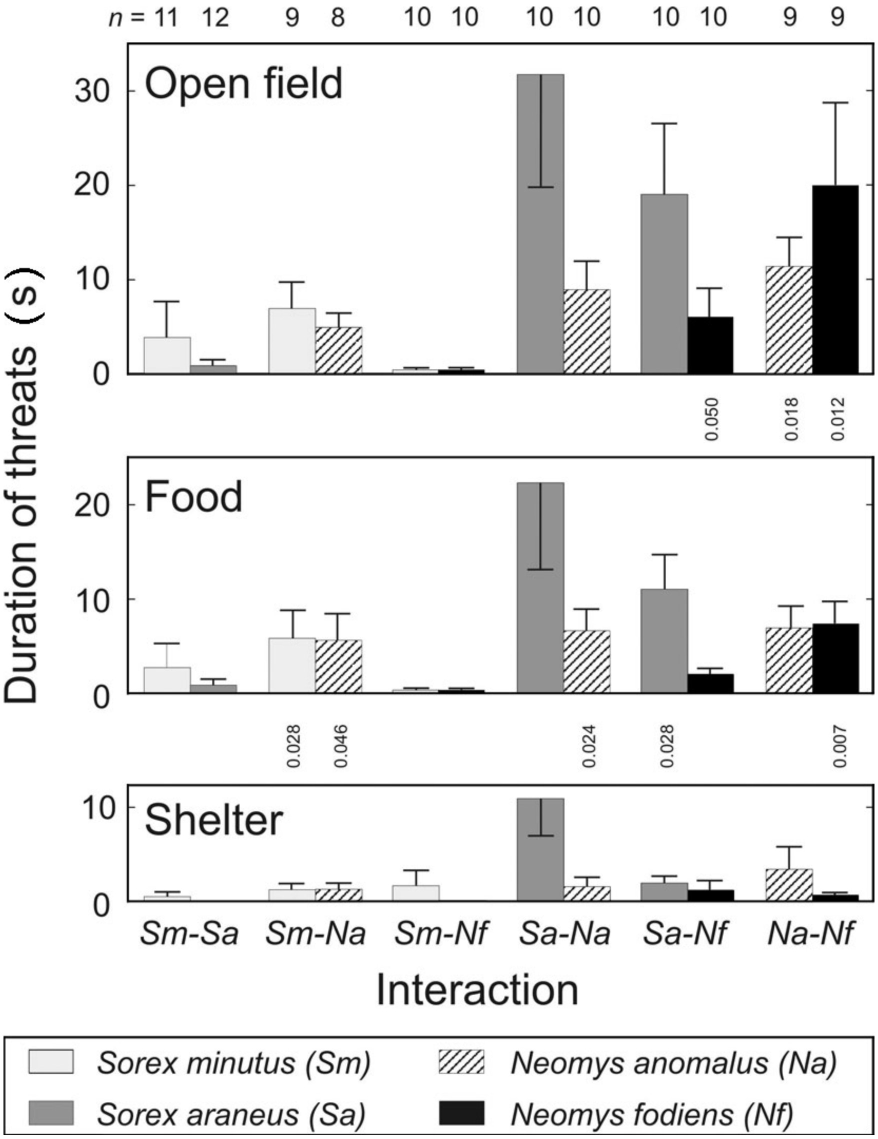
Fig. 4. Total duration (mean ± SE) of defensive behaviours displayed by shrews per 5 min during the three test stages. See Figs. 2 and 3 for further details.

bination in the shelter stage (U = 18.5, p = 0.018). *Neomys fodiens* attacked the other three species longer than vice versa (though the difference was insignificant in interactions with *N. anomalus*). Offensive behaviours of *N. anomalus* prevailed over those of the two *Sorex* species but not those of *N. fodiens*. Attacks of *S. araneus* prevailed only over those of *S. minutus*, and offensive behaviours initiated by *S. minutus* were shorter than those of the other species. Thus, ranking the species (from highest to lowest) according to the duration of offensive behaviours resulted in the following hierarchy: *N. fodiens*, *N. anomalus*, *S. araneus*, and *S. minutus*. When the levels of interspecific aggression were compared, *Neomys* species were more aggressive than *Sorex* species. The offensive behaviours initiated by *N. anomalus* towards *S. araneus* were particularly long (up to 22.1 s/5 min), and even in the shelter stage, remained at a high level (more than 5 s/5 min). The shortest total duration of attacks (0–0.8 s/5 min) was recorded in *S. minutus* (Fig. 3).

The duration of defensive behaviours (Fig. 4) was also very diversified among species in all stages of the tests (Kruskal–Wallis test, H = 56.011–73.194, p = 0.000, df = 11). They were always longer in the smaller of the two paired species. These differences were significant (after FDR) in every stage of the test and all pairs of compared species (Mann–Whitney U test, U = 0.0–24.5, p = 0.0002–0.017), the only exception being interactions between *S. araneus* and *N. fodiens* in the shelter stage (U = 27.5, p = 0.094). Regardless of the stage, defensive behaviours were shortest in *N. fodiens* (0.3–3.7 s/5 min) and usually longest in *S. minutus* (up to 28.7 s/5 min). However, they were longer in *S. araneus* when defending itself from *N. anomalus* in the open-field and food stages (33.2 and 23.6 s/5 min, respectively). *Sorex araneus* escaped from *N. anomalus* more often than vice versa, which suggests behavioural dominance of the latter. Thus, the dominance hierarchy based on the duration of escapes is identical with the one ranking species according to the duration of attacks: *N. fodiens* (dominant), *N. anomalus*, *S. araneus*, and *S. minutus* (lowest rank).

Also the duration of threats (Fig. 5) varied significantly among species in all stages of the tests (Kruskal–Wallis test,

Fig. 5. Total duration (mean ± SE) of threats displayed by shrews per 5 min during the three test stages. See Figs. 2 and 3 for further details.



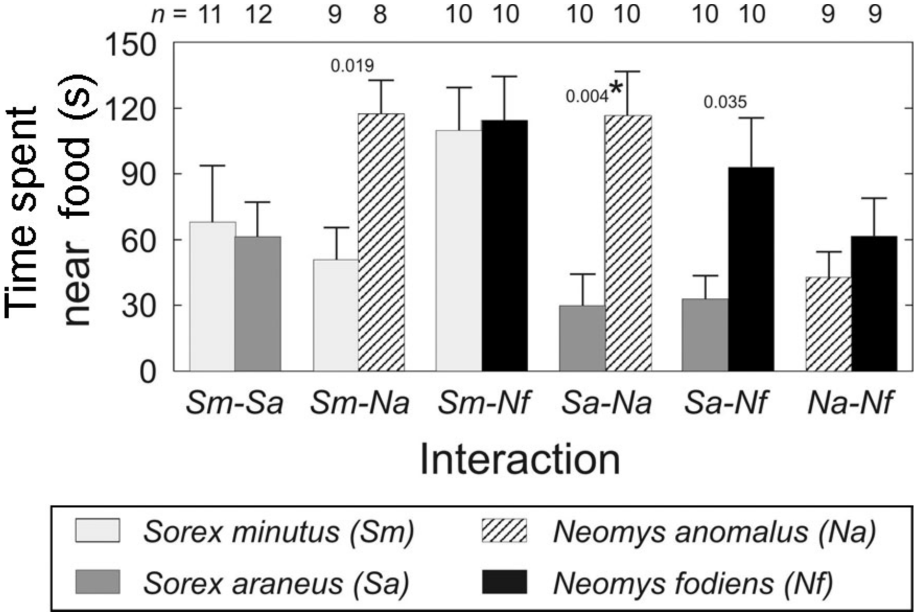
$H = 33.194–53.774$, $p = 0.000$, df = 11). In most paired species, the smaller one tended to spend a longer time threatening than the larger one. This suggests that threats expressed defensive rather than offensive activity, and indicated a subordinate species in a given combination. However, (*i*) in all test stages none of two-species comparisons exhibited a significant difference, (*ii*) in a few cases the larger species invested a similar or even longer time in making threats (*S. minutus* – *N. anomalus*, *S. minutus* – *N. fodiens*, and *N. anomalus* – *N. fodiens* interactions), and (*iii*) *S. minutus*, which theoretically should invest the longest time in making defensive threats, usually spent a shorter time on this activity than the other three species. Thus, it was not possible to rank the four species in a dominance hierarchy based on the duration of threats.

On the other hand, threats were particularly long in *S. araneus* interacting with *N. anomalus*, i.e., between the two species that are most similar in body mass (31.7 s/5 min in the open-field stage, 22.3 s/5 min in the food stage, and 10.9 s/5 min in the shelter stage; Fig. 5). The threats were, for example, significantly longer than those of *S. araneus* towards *S. minutus* in all test stages (Mann–Whitney *U* test, $U = 4.0–18.0$, $p = 0.0003–0.005$, valid after FDR). Threats of *S. araneus* towards *N. anomalus* remained long even after a shelter was introduced into the terrarium. Similarly, the threats made by *N. fodiens* were longest in interactions with the species that is most similar in body size, *N. anomalus*. In contrast, the shortest threats were recorded in interactions between *N. fodiens* and *S. minutus*. All this suggests that short threats during interspecific interactions indicate big differences in dominance rank, whereas long threats mean that the positions of a given pair of species in the dominance hierarchy are either close or not clear.

Competition for food and shelter

Contrary to our prediction, the presence of food and shelter did not increase competition and aggressiveness of shrews. In fact, the duration of agonistic behaviours gradually decreased throughout the food and shelter stages (Figs. 3–5). Even when this reduction was not very pro-

Fig. 6. Total time (mean ± SE) spent by shrews near food during the food test stage. See Figs. 2 and 3 for further details.



nounced in the food stage in some cases (e.g., offensive behaviours in *N. anomalus*, defensive behaviours and threats in *Sorex* species), most animals calmed down and the duration of conflicts dropped to nearly zero in the shelter stage.

As for offensive behaviours (Fig. 3), the reduction between the open-field and food stages was insignificant in all interactions, whereas between the food and shelter stages it was significant in all six cases in which *Neomys* species initiated attacks (Kruskal–Wallis test, H = 7.905–13.731, p = 0.019–0.001, df = 2; Wilcoxon test, Z = –2.366 to –2.809, p = 0.025–0.005, valid after FDR). In contrast, the interspecific offensive behaviours initiated by the two *Sorex* species were so short in all test stages that only one significant reduction was recorded: between the food and shelter stages in *S. araneus* interacting with *S. minutus* (Z = –2.375, p = 0.018). A reduction in the duration of defensive behaviours was displayed most clearly by the smaller (i.e., subordinate) of the two tested species (Fig. 4): it was insignificant in the comparison of the open-field stage with the food stage but significant in 7 out of 12 cases in the comparison of the food stage with the shelter stage (Kruskal–Wallis test, H = 6.316–14.541, p = 0.043–0.001, df = 2; Wilcoxon test, Z = –2.375 to –2.938, p = 0.018–0.003, valid after FDR). Also, the reduction in the duration of threats (Fig. 5) was more pronounced between the food and shelter stages than between the open-field and food stages, but no difference was significant after FDR adjustment.

Time spent near food (Fig. 6) varied significantly among species (Kruskal–Wallis test, H = 34.794, p = 0.000, df = 11). It was predicted that dominant species would spend more time eating and sniffing food than subordinate species. This was true for *N. anomalus*, which spent more time near food than its adversary in interactions with the smaller *S. minutus* ((Mann–Whitney U test, U = 11.0, p = 0.019) and *S. araneus* (U = 11.0, p = 0.004, significant after FDR), but not with the larger *N. fodiens*. *Neomys fodiens* visibly spent more time near food only in interactions with *S. araneus*. However, we found a tendency in *N. fodiens* that the lower the rank of its adversary in the dominance hierarchy, the more time it spent near food: the longest time was spent in tests with *S. minutus* (114.5 s, on average) and the shortest in trials with the strongest adversary, i.e., *N. anomalus* (61.4 s, on average). In contrast to our prediction, the smallest species, *S. minutus*, spent as much time near food as *S. araneus* and the large *N. fodiens*. Thus, these results did not allow us to determine a clear dominance hierarchy.

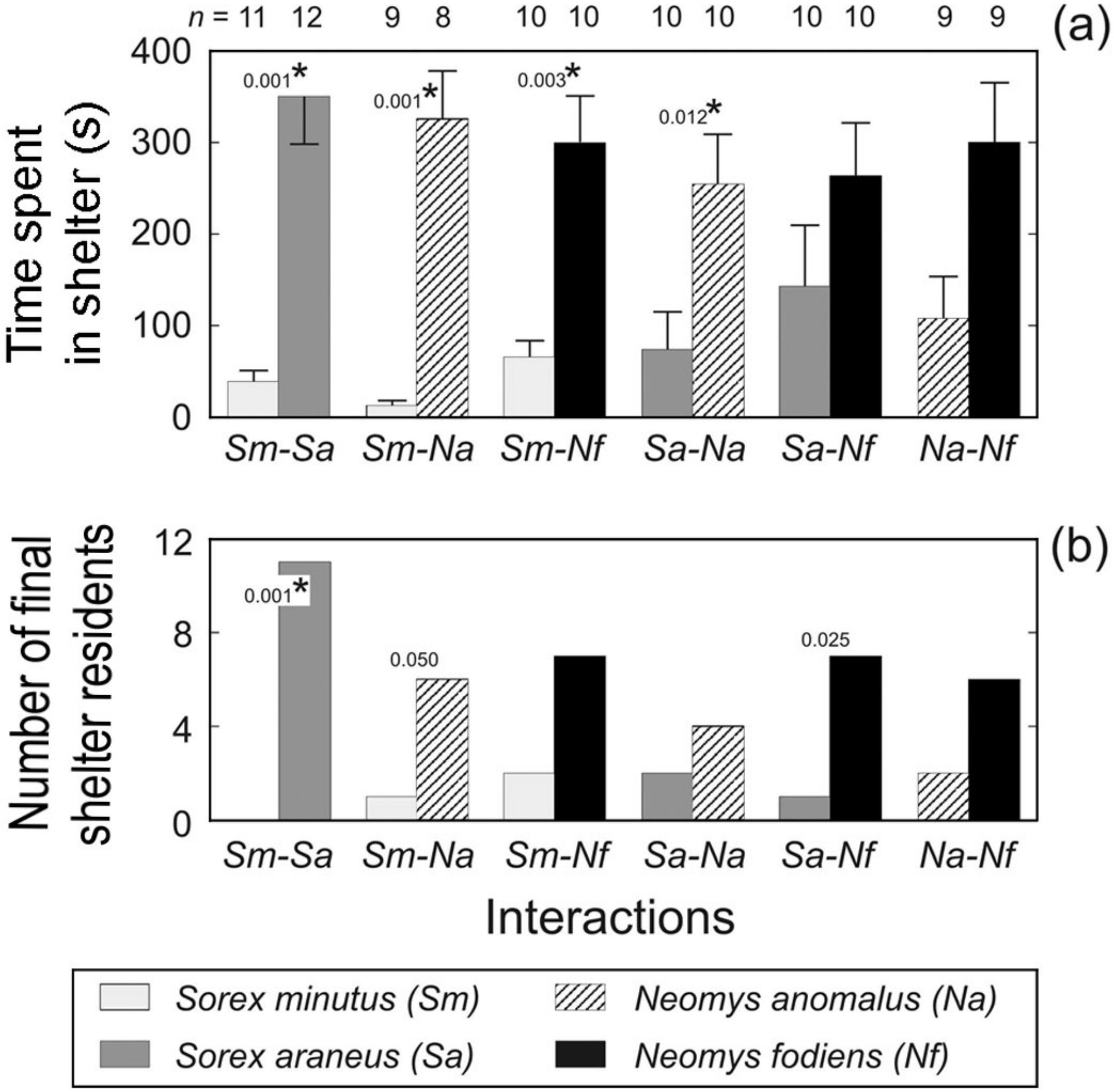
Time spent in the shelter (Fig. 7*a*) varied among species as well (Kruskal–Wallis test, H = 34.794, p = 0.000, df = 11). The individual belonging to the larger species always spent more time in the shelter than the smaller one (Fig. 7*a*). In four out of six interspecific combinations, the differences were significant (Mann–Whitney U test, U = 0.0–16.0, p = 0.001–0.012). Similarly, the larger of the two tested species remained more frequently in the shelter during the last minute of a trial (Fig. 7*b*). After the FDR procedure, the difference was significant only in the interaction between *S. minutus* and *S. araneus* (replicated goodness-of-fit test, G = 15.249, p < 0.001), but differences were clear also in four other combinations. The smallest difference was found in interactions between *N. anomalus* and *S. araneus* (G = 0.680, ns). Nevertheless, it was possible to determine a dominance hierarchy based on occupation of the shelter (from highest to lowest): *N. fodiens* > *N. anomalus* > *S. araneus* > *S. minutus*.

Discussion

Procedure and data set

Aggression between individuals belonging to different species may be much more context-dependent than can be recognized in laboratory experiments. When these individuals are living in their normal niche environments, the repertoire of their responses in potential encounters may be broader than in this test situation. For example, smaller spe-

Fig. 7. (*a*) Total time (mean ± SE) spent by shrews in the shelter during the shelter test stage. (*b*) Numbers of final shelter residents, i.e., shrews that remained in the shelter during the last minute of a test. Values at $p \leq 0.05$ for differences between pairs of compared species, revealed by Mann–Whitney *U* tests (*a*) and replicated goodness-of-fit tests (*b*) are shown. An asterisk indicates a significant difference after the levels of significance in both tests are adjusted using the false discovery rate procedure. See Fig. 2 for further details.



cies may take refuge from and avoid contact with larger species. However, experimental situations must be simplified to ensure adequate control over investigated variables. In our tests, a simplified environment was necessary to efficiently determine the order of behavioural dominance.

We tested most of our animals more than once. Unlike laboratory mice or rats, wild shrews are available in limited numbers (*N. anomalus* and *S. minutus*, especially, are difficult to collect in Białowieża Forest). Therefore, we were forced to use some individuals a few times. However, they were not used twice in the same species combination (with only three exceptions), and consecutive tests of the same individual were separated by at least 3 days. On the other hand, the procedure of repeated tests of the same individuals has been used in many experiments on rodents and shrews (e.g., Blaustein and Risser 1976; Ambrose and Meehan 1977; Cranford and Derting 1983; Dempster and Perrin 1990; Kalinin et al. 1998; Oleinichenko 2000) and, as recent studies suggest (Harper and Batzli 1997), it does not change their behaviour.

In the unchanging sequence of test stages (separated, open field, food, and shelter), the aggressiveness of shrews, contrary to our prediction, decreased gradually from stage to stage. We considered randomly changing the sequence of stages in every test to separate out the effects of habituation and fatigue. However, we were concerned that (*i*) such a procedure would increase the interindividual variation in behaviour; (*ii*) the results of tests with a different sequence of stages would not be fully comparable; (*iii*) the presence of shelter at an early stage of the test might determine and fix the dominance of one shrew over another, so that their interactions in subsequent stages would decline. Nevertheless, we acknowledge that our procedure could not verify conclusively whether competition for food or shelter increases interspecific aggressiveness.

Indicators of behavioural dominance

Based on the results of this study, we can propose reliable indicators and point out inadequate indicators of behavioural dominance in shrews. The dependable ones are total duration of attacks, total duration of escapes, total time spent in shelter, and occupation of shelter at the end of a trial. The behavioural patterns "keeping distance" and "to and fro", which typify subordinate individuals, also proved useful in analyses of dominance order (Rychlik and Zwolak 2005). In contrast, time spent near food and duration of threats proved to be inefficient indicators. The former seems to be influenced by differences in the energetic requirements of studied species. Contrary to our prediction, the smallest *S. minutus* spent a long time near food, even in tests with *N. fodiens*. However, *S. minutus* has the highest metabolic rate and the lowest resistance to starvation (Hanski 1984), so it was forced to feed frequently or for long periods, irrespective of the presence or rank of the competitor. On the other hand, the large *N. fodiens* could not exhaust its energy reserves during the 30 min tests, therefore it did not have to spend a long time feeding.

Indicators based on threats are defective because this behaviour occurs in both offensive and defensive contexts. In addition, it is often hard to distinguish between the two, as the meaning and function of some postures are unclear in shrews (Zwolak 2002). Thus, one cannot unequivocally associate this behaviour with dominance or subordination. In the present study, threats were frequently observed in both subordinate species (e.g., in *S. araneus* interacting with *Neomys* species) and dominant ones (e.g., *N. fodiens* tended to threaten more often than *N. anomalus* in the open-field stage). On the other hand, the total duration of threats may help to indicate which animals or species are of similar ranks in the dominance hierarchy. They were particularly long during interactions between the two species that are most similar in body size, *S. araneus* and *N. anomalus*. This supports our assumption that animals/species that are similar in strength threaten each other more often than animals/species with clearly separated positions in the dominance hierarchy.

Interspecific dominance

The dominance hierarchy determined using the above-mentioned indicators is as follows (from the highest to the lowest rank): *N. fodiens* > *N. anomalus* > *S. araneus* > *S. minutus*. Thus, in accordance with the prediction, body size is positively associated with position in the dominance hierarchy. This corresponds also to former findings on the dominance of *N. fodiens* over *N. anomalus* (Krushinska and Pucek 1989; Krushinska and Rychlik 1993, 1994; Krushinska et al. 1994) and *S. araneus* over *S. minutus* (Crowcroft 1955; Croin Michielsen 1966; Ellenbroek 1990; Dickman 1988, 1991; Ellenbroek and Hamburger 1991). However, in contrast to the above-mentioned studies, our study involved the entire shrew community and provides both qualitative and quantitative evidence, based on a relatively large and credible data set.

The larger *Neomys* species initiated (proportionally and in absolute terms) more active aggressive behaviours (such as offensive attacks, combats, chases) than the smaller *Sorex* species. In contrast, *Sorex* species initiated more defensive behaviours (retreats, escapes). In addition, *S. araneus*, particularly, displayed many passive threatening postures. Moreover, *Neomys* species initiated relatively more offensive behaviours, whereas *Sorex* species initiated more defensive behaviours also in intraspecific interactions, i.e., when size asymmetry was removed (L. Rychlik and R. Zwolak, in preparation). These results confirm our prediction and support the hypothesis regarding the divergent evolution of behavioural patterns in dominant and subordinate species.

It is not surprising that the dominant *N. fodiens* was only occasionally attacked by the smaller species. However, the fact that *S. minutus* was also rarely attacked was unexpected. There are two mutually nonexclusive explanations for this finding: (1) the position of *S. minutus* in the dominance hierarchy could be so low that conflicts ended at threats, and the bigger species did not have to actually fight; and (2) *S. minutus* efficiently avoided direct contact and conflicts (Dickman 1988, 1991; Rychlik and Zwolak 2005).

It appears that the dominance of *N. anomalus* over *S. araneus* is not considerable, because interactions between these two species were characterized by particularly numerous conflicts. Moreover, *S. araneus* occupied shelter at the end of trials only slightly less often than *N. anomalus* did. This similarity in their positions in the dominance hierarchy may be explained by the similarity in their body sizes. This result is consistent with the well-supported prediction that equal competitors are more likely than asymmetric ones to escalate conflicts (Maynard Smith and Parker 1976; Young 2003). On the other hand, our prediction that *N. anomalus* (being more social and thus potentially less aggressive and more tolerant) would occupy a lower position in the dominance hierarchy than *S. araneus* was not confirmed. Perhaps the higher than expected dominance rank of *N. anomalus* is a result of its stress-enhanced aggression. The high excitability of *N. anomalus* and its susceptibility to stress caused by unknown surroundings and an open field have been reported previously (Michalak 1982; Krushinska and Pucek 1989; Krushinska and Rychlik 1993; Krushinska et al. 1994). Under such conditions, the aggressiveness and number of conflicts initiated by *N. anomalus* increased, but dropped soon after these shrews acquainted themselves with their surroundings (Krushinska and Rychlik 1993; Krushinska et al. 1994) or immediately after shelters were offered (Krushinska and Pucek 1989). The same reactions (a high level of interspecific aggression in an open arena and a significant decrease of mutual antagonism when a shelter became available) were demonstrated in rodents (e.g., Ambrose and Meehan 1977; Putera and Grant 1985).

If the sizes of the interacting species are similar, dominance and subordination may depend on the place of interaction rather than the species involved. In such instances we are dealing with interspecific territoriality. For example, in interactions between two rodent species (*Peromyscus leucopus* (Rafinesque, 1818) and *Peromyscus maniculatus* (Wagner, 1845)), individuals that resided on their territory dominated (Wolff et al. 1983). Other cases of interspecific territoriality are known in the family Soricidae (e.g., *Sorex* *vagrans* Baird, 1857 and *Sorex monticolus* Merriam, 1890, (Hawes 1977); *S. araneus* and *Sorex coronatus* Millet, 1828 (Neet 1989)). The dominance hierarchy demonstrated in the present study is based on interactions that took place in a site that was unfamiliar to both adversaries (neutral arena). Since *S. araneus* is intra- and inter-specifically territorial (e.g., Croin Michielsen 1966; Neet 1989), we cannot rule out the possibility that in the wild, *S. araneus* is dominant, within its territory, over *N. anomalus*.

Interference competition

Many studies have shown that interspecific aggression among rodents reflects the interference competition that influences their space or habitat use, circadian activity, fitness, etc. (Grant 1970, 1972; Frye 1983; Lemen and Freeman 1983; Falkenberg and Clarke 1998; Eccard and Ylönen 2002). Similarly, according to Dickman (1991), interference competition is recognized as an important factor structuring communities of shrews. He suggests that for the dominant species the cost of interference is negligible, but after it secures exclusive access to the resource-rich microhabitat, the profit is high. For the subordinate species, the benefits from temporary use of the same rich microhabitat often exceed the costs of the necessary vigilance and escapes to a nearby refuge. However, the absence of a shrew species in a particular habitat may be due to interference competition with larger species (Hanski and Kaikusalo 1989). Nevertheless, it can be accepted that interference competition is one of the mechanisms that also shapes the niches and fitness of shrew species coexisting in wet habitats of Białowieża Forest. And then, interspecific aggression may be an outcome, rather than a cause, of the interspecific relations in a given community.

Based on the observed order of dominance, we suppose that the effects of interference competition from other shrew species are negligible only for the dominant *N. fodiens*. However, this species probably does incur the costs of chasing away its smaller competitors, or the costs resulting from its exploitation of shared resources. For subordinate species, their movements, space use, feeding, and use of shelters can be restricted. In our study, dominant animals restricted the access of subordinates to the shelter but, unexpectedly, not to the food. This was probably related to the experimental design. During the trials, shelter was needed much more than food because the animals remained in an unfamiliar, open, and bright space. On the other hand, owing to the short duration of the trials, there was no absolute need to forage, especially in the case of the larger species, because the energetic reserves of shrews increase with body size (Hanski 1985). Furthermore, we cannot exclude the possibility that a longer period of separation and open-field encounters may have allowed the habituation rate to stabilize, thus improving baseline conditions for detecting any subsequent increase in aggression when the food resources were added. Competition for shelter has only rarely been studied. *Neomys anomalus* occupied shelters communally more frequently when it was kept in enclosures together with *N. fodiens* than when kept alone (Krushinska and Rychlik 1993). Considering the rarity of communal nesting in Soricinae, such a change in behaviour is significant.

Neomys anomalus is probably subjected to strong interference from both *N. fodiens* and *S. araneus*. In areas of allopatry, *N. anomalus* lives close to water (e.g., in Turkey, Kryštufek et al. 1998; Kryštufek and Vohralík 2001; in Portugal, Rychlik and Ramalhinho 2005), whereas in sympatry, *N. fodiens* presumably displaces *N. anomalus* from microhabitats that are very wet and located beside water (Rychlik 2000, 2001). At the same time, in drier places *N. anomalus* meets *S. araneus*, the numerically dominant species. We found that *N. anomalus* dominated behaviourally over *S. araneus*, but this supremacy was only slight and was hard-won. Thus, the costs of interference competition may be especially high in this species. These costs might explain why everywhere in central Europe the densities of *N. anomalus* are lower than those of *N. fodiens* and *S. araneus* (Dehnel 1950; Aulak 1970; Niethammer and Krapp 1990; Mitchell-Jones et al. 1999; Rychlik 2000; L. Rychlik, unpublished data).

The differences in microhabitat preferences of the four studied species are known (Rychlik 2000). To determine the role of interspecific competition on microhabitat selection, a removal experiment is required. This consists of removing one of the coexisting species in order to detect subsequent changes in the niches of the other species (e.g., shifts in diet, space use, patterns of circadian activity, etc.). Dickman (1988) conducted such an experiment in a two-species community composed of *S. minutus* and *S. araneus*. His results indicated that *S. araneus* displaced *S. minutus* from places with abundant large prey (preferred by both species) and suggested interference, not exploitation, as the mechanism of competition. Currently, similar studies investigating a four-species community of shrews have been conducted in Białowieża Forest, and the preliminary results suggest that interference competition indeed occurs there and is stronger between *N. fodiens* and *N. anomalus* than between *N. fodiens* and *S. araneus* (Rychlik et al. 2004). The final results of those studies, combined with the findings of the present study, will help to answer questions about the importance and mechanisms of competition among species of Soricidae.

Conclusions

The present study showed interspecific differences in social behaviour, determined the order of behavioural dominance within the community (*N. fodiens* > *N. anomalus* > *S. araneus* > *S. minutus*), and identified reliable (duration of offensive and defensive behaviours, time spent in shelter) and unreliable (duration of threats, time spent near food) indicators of interspecific dominance. With regard to the tested hypotheses and predictions: (*i*) the level of aggression was higher in larger species, thus dominance rank seemed to be positively correlated with body size at the specific level; (*ii*) the larger *Neomys* species were more aggressive and initiated relatively more offensive behaviours, whereas the smaller *Sorex* species initiated more defensive behaviours; (*iii*) the level of aggression and dominance rank of *N. anomalus* (the gregarious species) were not lower than expected according to its body size, therefore this study did not prove that aggressiveness and dominance rank are influenced by the social organization of a given species; (*iv*) this study also did not show that competition for food or shelter increased interspecific aggressiveness; however, (*v*) individuals of dominant species spent more time in shelter than individuals of subordinate species, therefore dominant species restricted the access of subordinate species to resources (shelter under these experimental conditions).

Acknowledgments

We are very grateful to A. Arasim, M. Babski, K. Bochowicz, I. Smerczyński, and E. Sorato for their field and technical assistance, M. Konarzewski for help with statistical analyses, and I. Ruczyński, L.C. Drickamer, and the anonymous reviewer for their helpful comments on our manuscript. J. Kamler kindly improved our English. This study was supported by grant No. 6 P04F 036 21 from the Committee for Scientific Research, and by the Mammal Research Institute of the Polish Academy of Sciences and Adam Mickiewicz University.

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