Acta Theriologica 50 (3): 289–308, 2005.
PL ISSN 0001–7051

Behavioural mechanisms of conflict avoidance among shrews

Leszek RYCHLIK and Rafał ZWOLAK*

Rychlik L. and Zwolak R. 2005. Behavioural mechanisms of conflicts avoidance among shrews. Acta Theriologica 50: 289–308.

Stable co-existence of similar species should be facilitated by mechanisms impairing, besides exploitative, interference competition. We investigated avoidance of intra- and interspecific conflicts in a four-species community of shrews [*Sorex minutus* Linnaeus, 1766, *S. araneus* Linnaeus, 1758, *Neomys anomalus* Cabrera, 1907, and *N. fodiens* (Pennant, 1771)], using the method of dyadic encounters in a neutral arena. We tested whether the use of passive (habituation, reduction of mobility, increase of inter-individual distance, and stillness) and active ('to-and-fro' and 'keeping distance' behaviours) forms of conflict avoidance depends on species, size or domination rank. The duration of conflicts was positively correlated with mobility and negatively with inter-individual distance, whereas it was unrelated to time of stillness and the active forms. The repertoire of conflict avoidance mechanisms was not species-specific and the display of these mechanisms depended rather on the size and domination rank of animals participating in a given interaction. In contrast to rodents, shrews did not avoid conflicts by the most passive forms: freeze and stillness reactions. All other forms were used with a higher or lower efficiency by all species. However, consistent with our predictions, large shrews (as *N. fodiens*) used mainly the passive mechanisms of conflicts avoidance ('wait-and-see' strategy), whereas small shrews (as *S. minutus*) invest proportionally more time in active forms ('escape' strategy).

Mammal Research Institute of the Polish Academy of Sciences, Waszkiewicza 1, 17-230 Białowieża, Poland, e-mail: lrychlik@bison.zbs.bialowieza.pl (LR); Department of Systematic Zoology, Institute of Environmental Biology, Adam Mickiewicz University, Fredry 10, 61-701 Poznań, Poland (RZ)

Key words: *Neomys*, *Sorex*, aggression avoidance, agonistic behaviour, stable coexistence, dyadic encounters, interference competition

Introduction

Although interspecific competition is for many years in the centre of ecologists' attention, most research focused so far on the exploitation rather than interference competition in small mammals, and much more is known about competition among rodents than shrews (Schoener 1983, Kirkland 1991, Eccard and Ylönen 2002, 2003). Interference competition occurs when some individuals directly (eg by fighting) reduce the access of other individuals to limited resources (Feldhammer *et al.* 1999). Aggression and competition often occur together in time and space,

---

* Present address: Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA

and aggression seems to be primarily an adaptation to cope with competition (Moynihan 1998). Experiments performed on different mammals demonstrated both direct aggression contributing to interspecific competition (eg Grant 1970, 1972, Frye 1983), as well as interspecific tolerance and non-competitive co-existence (eg Wolff and Dueser 1986, Perri and Randall 1999). Usually, aggression is higher between sympatric and closely related species than between allopatric and unrelated ones (Nevo *et al.* 1975, Dempster and Perrin 1990). On the other hand, interspecific territoriality, aggression and communication help in keeping sympatric species ecologically separate (Blaustein and Risser 1976, Hawes 1977), structuring communities (Perri and Randall 1999), but also in reduction of conflicts (Poduschka 1977, Movchan and Shibkov 1981, Archer 1988), and thus facilitate stable coexistence of competitors.

Soricinae shrews seem to be an excellent model to investigate competition for food and space because: (1) they usually coexist in multi-species communities (Kirkland 1985, 1991, Churchfield *et al.* 1999, Sheftel and Hanski 2002); (2) their metabolic rates and food requirements are the highest among mammals (Vogel 1976, McNab 1991, Taylor 1998); (3) they are intra- and interspecifically aggressive, intolerant and territorial (Rychlik 1998); (4) they are very sensitive to different biotic and abiotic factors as changes in prey availability, population density, temperature or humidity (Hanski 1994, Gliwicz and Taylor 2002). All of these characteristics require particularly effective mechanisms of resource partitioning. Furthermore, conflicts among shrews are common under natural conditions (Churchfield 1990, L. Rychlik and R. Zwolak, pers. obs.).

In the wet habitats of Białowieża Forest (eastern Poland) two terrestrial species of Soricinae shrews (the pygmy shrew *Sorex minutus* Linnaeus, 1766 and the common shrew *S. araneus* Linnaeus, 1758) co-exist with two semiaquatic ones [the Mediterranean water shrew *Neomys anomalus* Cabrera, 1907 and the Eurasian water shrew *N. fodiens* (Pennant, 1771)]. They form a guild (Schröpfer 1990), thus intra- and interspecific competition for resources is very likely. Previous studies on niche segregation among these species have included research on foraging modes (Rychlik 1997), food preferences and handling (Rychlik and Jancewicz 1998, 2002), trophic niches (Churchfield and Rychlik, in press), microhabitat preferences (Rychlik 2000, 2001), and patterns of circadian activity (Rychlik 2005). Because considerable overlap in different niche dimensions (the mentioned studies) and high population densities (L. Rychlik, unpubl.) were found, frequent direct contacts seem to be inevitable within this shrew community. Such contacts usually result in agonistic interactions (Crowcroft 1955, Croin Michielsen 1966, Krushinska and Pucek 1989, Zwolak and Rychlik 2004). In this situation, the existence of efficient mechanisms of conflict avoidance or aggression reduction is of great importance for stable coexistence of these species.

In our other study (L. Rychlik and R. Zwolak, in prep.) we described the order of dominance among these species (*N. fodiens* > *N. anomalus* > *S. araneus* > *S. minutus*) and their intra- and interspecific aggression. This aggression is probably associated with the defence of resources, as the food niches of these shrews overlap to a great extent (Churchfield 1984, Churchfield and Rychlik, in press). Because aggressive interference is costly in terms of time and energy, it could be expected that some mechanisms facilitating coexistence should evolve (Moynihan 1998, Perri and Randall 1999). Movchan and Shibkov (1981, 1987) indicated that acoustic communication serves as such a mechanism in shrews, but olfactory communication also plays a role (Hawes 1976, Platt 1976, Poduschka 1977, Shchipanov and Oleinichenko 1993, Cantoni *et al.* 1996). Other mechanisms found previously were: (1) habituation, (2) learning the presence of dominants and avoidance of their aggression, (3) group occupation of shelters (in interactions between *N. anomalus* and *N. fodiens* – Krushinska and Rychlik 1993, Krushinska *et al.* 1994), (4) maintaining distance (interactions of *S. minutus* with *S. araneus* – Crowcroft 1955, Dickman 1991). However, our preliminary analysis (Zwolak and Rychlik 2004) gave an unclear conclusion about the role of mobility reduction. Thus, the subject of conflict avoidance still needs a thorough study.

The goal of the present study was to investigate some behaviours that might function as mechanisms diminishing aggression or increasing tolerance or spacing of these (and other) sympatric species. Starting with three hypotheses, we derived several predictions. First, shrew (especially the subordinate individuals or species) should tend to reduce aggression in their opponents, as well as frequency and duration of conflicts with them, in order to avoid injures and losses of time and energy, which could result in significant losses of fitness (Moynihan 1998). Consequently, we expected a decrease in number and duration of conflict with passage of time of interaction. Alternatively, aggressiveness of opponents could increase and lead to wounds or death (Enquist and Leimar 1990).

Second, since interspecific interference competition is often asymmetric (Schoener 1983), dominant and subordinate species may optimize their behaviour in different ways (Maynard Smith and Parker 1976, Law *et al.* 1997). According to the theory, large-dominant species should evolve active and offensive behaviours (direct attacks, fighting), whereas small-subordinate species should develop rather passive and defensive forms (escapes, ritualized threats; Persson 1985, Young 2003). Therefore, we predicted that subordinate species (*S. minutus*, *S. araneus*) will display more frequently and more differentiated repertoire of behaviours leading to conflict avoidance than dominating species (*N. fodiens*, *N. anomalus*). An alternative hypothesis was that the repertoire of these behaviours is not species or size specific.

Third, the tested mechanisms of aggression avoidance could be grouped into two categories: (1) passive that includes habituation, increase of inter-individual distance, reduction of mobility, and increase of stillness, and (2) active including keeping distance and to-and-fro behaviours (definitions in 'Material and methods'). Because of the very high rate of metabolism, high activity and tense energetic budget, shrews should display active rather than passive forms of aggression avoidance. However, the great differences in body sizes of the tested shrews (eg *N.*

fodiens is about 5 times larger than *S. minutus*) will lead to interspecific differences in behaviour. The greater the shrew and energy stores in its body, the stronger tendency for passive forms of aggression avoidance, ie for 'wait-and-see' strategy. The smaller the shrew and energy stores in its body, the stronger tendency for active forms of aggression avoidance, ie for 'escape' strategy. It is because small shrews need to 'solve' the problem quickly to resume foraging. We also expected that duration of conflicts would be positively correlated with mobility and negatively with inter-individual distance, stillness, keeping distance and to-and-fro behaviours.

Thus, the aims of this study were: (1) To investigate what mechanisms of conflict avoidance function among these shrew species. (2) To check if the repertoire of these mechanisms is wider in smaller than larger species. (3) To test if the tendency to display active forms of conflict avoidance is stronger in smaller than larger species. (4) To verify if the forms and efficiency of conflict avoidance are species specific or rather depend on the rank of animal in a given interaction (ie if it is subordinate or dominant).

Material and methods

Catching and maintaining the animals

Wild shrews were live-trapped with pitfalls in wet habitats of the Białowieża Forest (E Poland) between June and September. Pitfalls contained a handful of moss for bedding, a tea-spoon of minced beef as bait/food and were covered with a roof to protect them from rain. The traps were opened in the afternoon (usually about 17:00 hrs) and checked every 2–2.5 hours till early night-hours (usually till 24:00 hrs). Trapping was not performed during heavy rainfalls and cold evenings. Pregnant and lactating females were caught very rarely and were released immediately at the place of capture. Animals were transported in buckets containing some cotton bedding and food (minced beef and/or fly larvae). Transportation by car or bicycle lasted 10–20 minutes. In the laboratory, shrews were placed in individual cages (30 40 15 cm), where they acclimatised to the captive conditions for at least 5 days. The cages were equipped with a shelter (a reversed 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 of them were kept ca 3 weeks and only 9 animals were kept longer than 4 weeks.

Testing procedure

Due to the shrews' cryptic life, it was impossible 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 interactions among rodents (eg Dempster and Perrin 1990, Harper and Batzli 1997, Johannesen *et al.* 2002) and shrews (eg Krushinska and Pucek 1989, Baxter and Irwin 1995, Kalinin *et al.* 1998).

A total of 69 subadult animals (ie this year's fully grown, but sexually immature shrews) were used in dyadic encounters: 17 individuals of *S. minutus*, 19 of *S. araneus*, 15 of *N. anomalus*, and 18 of *N. fodiens*. Animals were tested in a separate room during daytime, usually between 09:00 and 16:00 hours, ie during the period of decreased activity of shrews (Rychlik 2005). An intra- or interspecific pair of animals was placed in neutral arena, that is a glass terrarium measuring 70 30 40 cm (Fig. 1), and their behaviour was video-recorded. Sony SSC-C370P camera, Panasonic

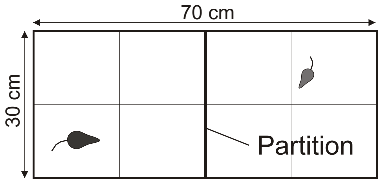

Fig. 1. The scheme of the experimental terrarium. Note the lines dividing the floor into rectangles used for measure inter-individual distance and mobility of shrews.

Table 1. The number of tests (in brackets: n – number of obtained results) in particular intra- and interspecific combinations. * – 11 results for *S. minutus* and 12 for *S. araneus*. ** – 9 results for *S. minutus* and 8 for *N. anomalus*.

	S. minutus	*S. araneus*	*N. anomalus*	*N. fodiens*
S. minutus	3 (6)			
S. araneus	12 (11/12*)	5 (10)		
N. anomalus	9 (9/8**)	10 (10)	5 (10)	
N. fodiens	10 (10)	10 (10)	9 (9)	5 (10)

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 hung about 1.5 m above. After each test, the terrarium was carefully washed with a detergent.

Each test lasted 30 minutes and consisted of four consecutive parts. During the first 5 minutes, the animals stayed in the different halves of the terrarium, separated by a transparent partition made of Plexiglass (Fig. 1). Shrews could settle in after removal from individual cages and explore the new surroundings. In other studies, this period was similar or shorter: 1–5 minutes (eg Krushinska and Pucek 1989, Baxter and Irwin 1995, Harper and Batzli 1997). Then the partition was removed and the animals could interact in so called ‘neutral open field’. After 5 minutes, a bowl with minced meat was placed in the terrarium for 10 minutes. In the fourth part (the last 10 minutes of test), the bowl was replaced with a shelter (a reversed pot). Meat and shelter were placed in the terrarium for reasons of other investigations (L. Rychlik and R. Zwolak, in prep.).

Immediately after trials, animals were weighed to 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 measures), 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 78 trials were conducted. The number of tests per each species combination is presented in Table 1. Each individual took part in 1–4 tests (mean 2.3), but each time with a different species. The only exceptions were made by the participation of one of the Mediterranean water shrews in two tests with pygmy shrews and one pygmy shrew in two tests with common shrews. In both cases, we took into account only the first from these two trials (Table 1). Consecutive tests of the same individual were separated by at least a 3-day break.

Conflicts and avoidance mechanisms

The following categories of shrew behaviour were analyzed: (1) Conflicts – classified in accordance with previous studies (Olsen 1969, Martin 1980, Baxter and Irwin 1995, Shchipanov *et al.* 1998). They included (a) 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 close distance), and follow (slower, at some distance); (b) defensive behaviours: retreating, jumping away and escaping (ie running away), all as a result of direct contact; (c) threats: stance, tripedal, sideways, back and upright postures, and threatening vocalization. In analyses, all kinds of conflicts were pooled. (2) Inter-individual distance index – using lines drawn on the floor of the terrarium (which divided it to eight equal rectangles; Fig. 1), the distance between tested shrews was recorded every 15 seconds. The distance index ranged from 0 (two shrews within the same rectangle) to 4 (shrews in the most-distant, diagonal rectangles). (3) Mobility index – loco-motor activity defined as the number of moves from one rectangle to another (ie the number of lines crossed by an animal) during 5 minutes. (4) Stillness – included 'attend' (shrew active but at site, without loco-motor activity) and 'freeze' (motionless except vibrissae and snout). (5) Active avoidance – 'keeping distance behaviour' (simultaneous movements of the given shrew in more or less constant distance from the adversary) and 'to-and-fro behaviour' (running up to the adversary that is immediately followed by quick withdrawal). These two behavioural categories were pooled in analyses. Duration of a single act of conflicts, stillness and active avoidance was measured with the accuracy of 1 second.

Data analysis

We analyzed conflict avoidance by comparing shrews' behaviour observed during two phases: phase I – the first 5 minutes of the interaction (ie from 1st to 5th minute after removal of the partition) and phase II – the third 5 minutes of the interaction (ie from 10th to 15th minute after removal of the partition). Separately for phase I and II of each test, the durations of conflicts, stillness and active avoidance were summed and expressed as total duration per 5 minutes. The mean inter-individual distance during these 5-minute periods was also calculated. Then, the results of all trials in a given pair of species were averaged and these averages are presented on graphs along with standard errors. In statistical analyses, intraspecific differences were compared using Wilcoxon tests, whereas interspecific or inter-combination differences were tested using Mann-Whitney *U*-tests (Sokal and Rohlf 1995). Relationships between chosen categories of behaviour were tested using Pearson correlation and regression analysis. Our analysis of this material was enhanced by the following computer programs: Observer Video-Pro ver. 4.1, FoxPro ver. 2.5b, MS Excel '97, GraphPAD InStat ver. 1.13, and SYSTAT ver. 5.03.

Results

In all interactions, duration of conflicts was shorter during phase II than I (Fig. 2), and this difference was statistically significant in five cases (Wilcoxon test: $Z = -2.429$ to -2.805, $p = 0.015$ to 0.005). Decrease in the duration of conflicts was proportionally greater in intra- than interspecific interactions. Among intraspecific interactions (Fig. 2, left side), duration of conflicts was especially long in *N. anomalus*. It was significantly longer than in the three other species during phase I (Mann-Whitney *U*-test: $U = 21.5$ to 6.5, $p = 0.058$ to 0.001). However, in phase II duration of conflicts among *N. anomalus* so decreased that it was longer only than conflicts among *S. araneus* ($U = 10.0$, $p = 0.003$). Among interspecific interactions (Fig. 2, right side), the duration of conflicts in *S. minutus*-*S. araneus* and *S. minutus*-*N. fodiens* pairs was shorter than in the other interspecific contacts (differences were significant in all comparisons in phase II and in all comparisons with the exception of *S. araneus*-*N. fodiens* in phase I; $U = 26.0$ to 4.0, $p = 0.076$ to 0.0006).

In contrast to the prediction, the distance between tested animals did not change between phase I and II (Fig. 3). *Neomys anomalus* tended to stay in a shorter inter-individual distance than the three other species in intraspecific interactions, as well as interspecific interactions with a weaker opponent (eight

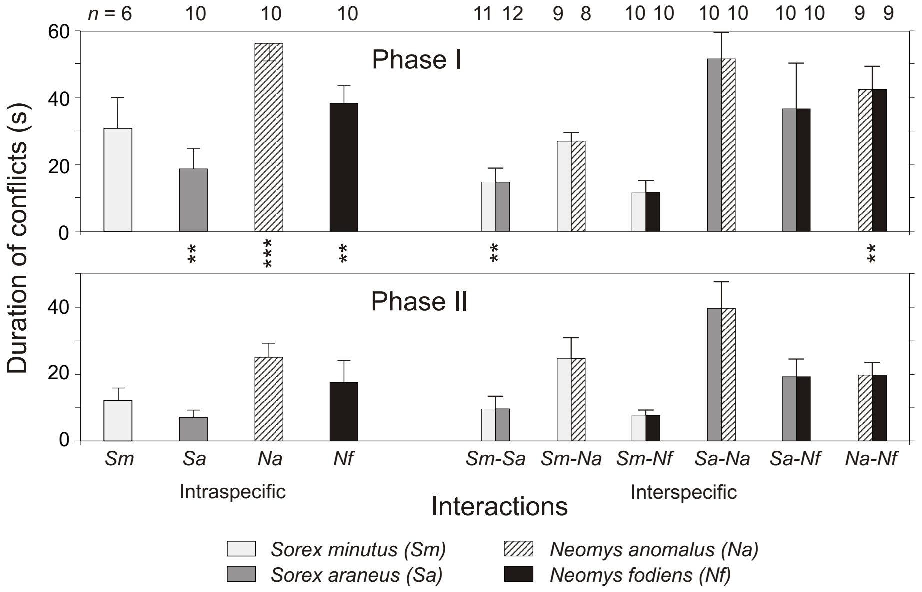

Fig. 2. Mean (+SE) total duration of conflicts displayed by shrews per 5 minutes during the two phases of interactions. Significant intraspecific differences between the phases (revealed by Wilcoxon test) are shown between the panels: ** *p* 0.01, *** *p* 0.005. *n* – sample size.

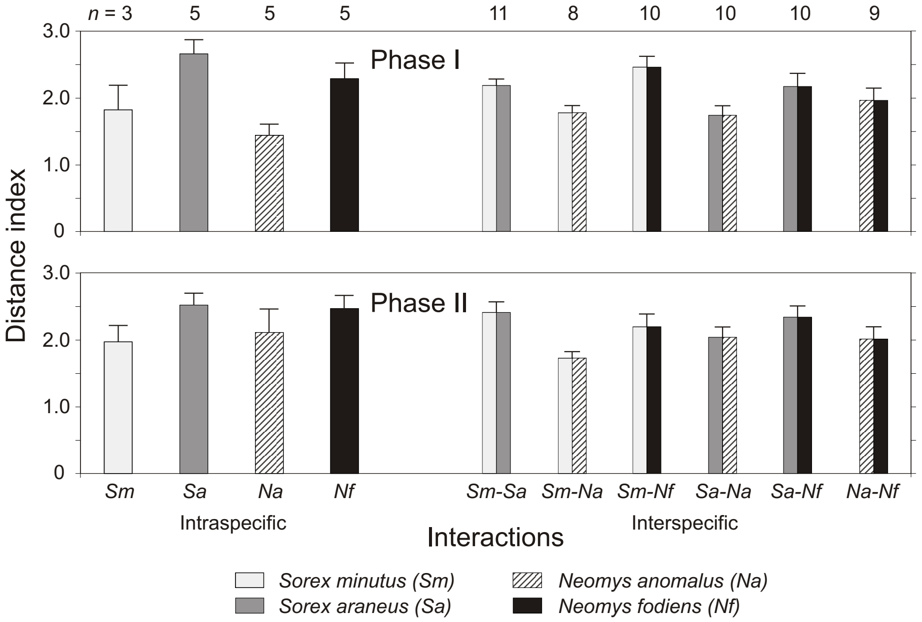

Fig. 3. Mean (+SE) inter-individual distance displayed by shrews during the two phases of interactions. See Fig. 2 for more explanations.

comparisons showed significant differences; Mann-Whitney *U*-test: $U = 23.0$ to 0.0, $p = 0.027$ to 0.009).

In all interactions, mobility was lower in phase II than I (Fig. 4). The reduction was statistically significant in almost all cases (Wilcoxon test: $Z = -1.988$ to -2.803, $p = 0.047$ to 0.005). In interspecific interactions, the reduction of mobility occurred only in subordinate (*S. minutus*-*N. fodiens* and *N. anomalus*-*N. fodiens* interactions) or was more pronounced in subordinate than dominant species (*S. minutus*-*N. anomalus* and *S. araneus*-*N. anomalus* interactions). The order of species from the most to the least mobile was: *N. anomalus* > *S. minutus* > *S. araneus* > *N. fodiens*. The mobility of *N. anomalus* was significantly higher than that of its opponents in almost all interspecific interactions (Mann-Whitney *U*-test: $U = 18.5$ to 9.0, $p = 0.019$ to 0.011). It was also high in intraspecific interactions.

Although duration of stillness usually increased from phase I to II (Fig. 5), this increase was insignificant, with an exception of *S. araneus* interacting with *N. anomalus* (Wilcoxon test: $Z = 2.701$, $p = 0.007$). Moreover, a significant decrease occurred in the reaction of *N. anomalus* to *S. minutus* ($Z = -2.023$, $p = 0.043$). In intraspecific interactions, the tendency to remain still increased with body size (*S.

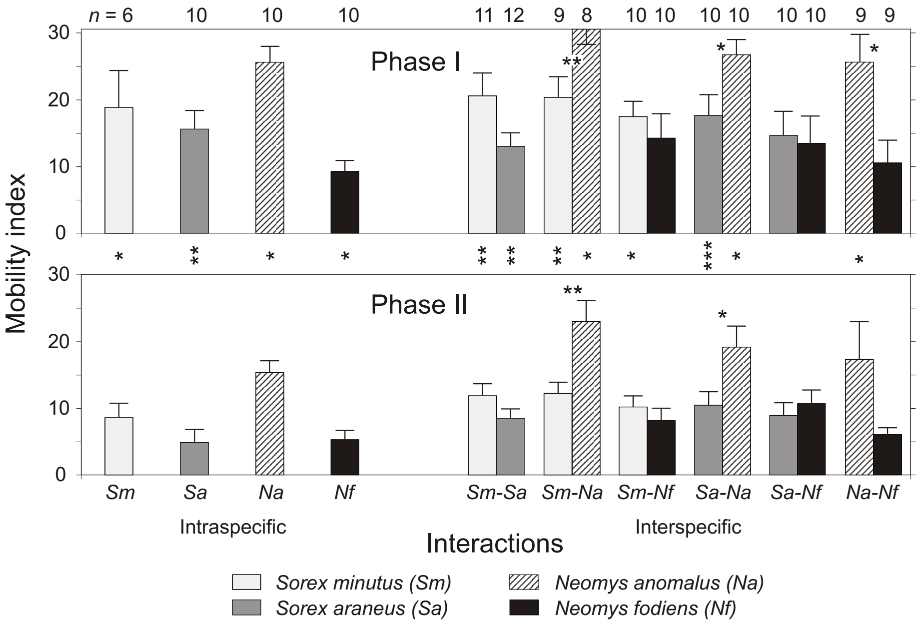

Fig. 4. Mean (+SE) moblity displayed by shrews per 5 minutes during the two phases of interactions. In interspecific interactions, behaviours of the two opponents are illustrated by separate bars; for example, in "*Sm-Sa*" combination the left bar represents behaviour displayed by *Sorex minutus* at presence of *S. araneus*, whereas the right bar shows behaviour displayed by *S. araneus*. Significant differences between interacting species (revealed by Mann-Whitney *U*-test) are shown over bars within the panels. Significant intraspecific differences between the phases (revealed by Wilcoxon test) are shown between the panels. For both tests: * *p* 0.05, ** *p* 0.01, *** *p* 0.005.

minutus < *N. anomalus* < *N. fodiens*), with the exception of *S. araneus*, which displayed the longest times of stillness. In the three kinds of interspecific interactions (*S. minutus*-*N. anomalus*, *S. araneus*-*N. anomalus* and *S. araneus*-*N. fodiens*) in both phases I and II, the subordinate species, consistent with our prediction, remained still longer than the dominating species. These differences were statistically significant except for the pair *S. araneus*-*N. fodiens* in phase I (Mann-Whitney *U*-test: $U = 21.0$ to 7.0, $p = 0.034$ to 0.001). However, in the three other kinds of interactions the duration of stillness was longer (though insignificantly) or similar in dominant than subordinate species. Only in *N. anomalus*, duration of stillness increased with the increase of body size of the opponent (Fig. 5).

Of particular interest, freezing occurred in *S. araneus* and *N. fodiens* (in their intra- and all interspecific interactions), and was not observed in *S. minutus* and *N. anomalus*. Duration of freeze ranged from 1.2 to 38.2 seconds per 5 minutes in *S. araneus* and from 0.0 to 31.8 seconds in *N. fodiens*. Duration of freezing was in five cases higher, and in three cases lower, in phase II than I, but no difference was significant.

In contrast to our prediction, the duration of active avoidance (keeping distance and to-and-fro behaviours) did not increase between phase I and II (Fig. 6). Instead, it rather decreased and the reduction was significant in two cases (Wilcoxon test: $Z = -2.082$ and -2.497, $p = 0.037$ and 0.013). In intraspecific interactions, all species displayed similar durations of active avoidance (in both

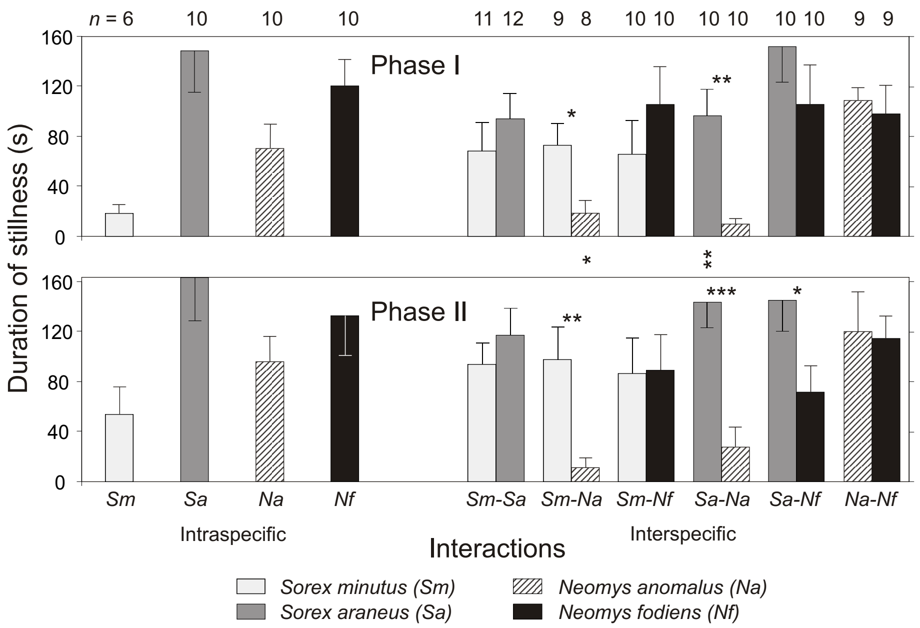

Fig. 5. Mean (+SE) total duration of stillness displayed by shrews per 5 minutes during the two phases of interactions. See Fig. 4 for more explanations.

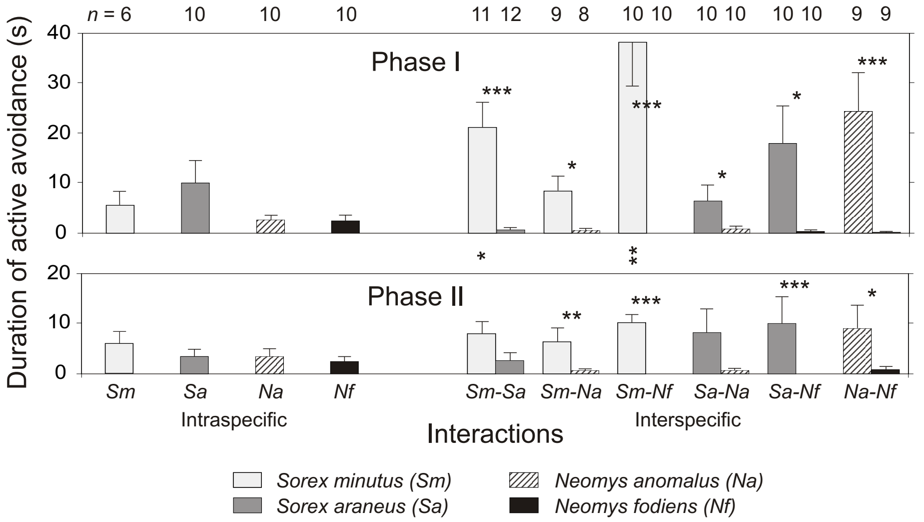

Fig. 6. Mean (+SE) total duration of active avoidance of conflicts displayed by shrews per 5 minutes during the two phases of interactions. See Fig. 4 for more explanations.

phases, all differences between species were statistically insignificant). In all interspecific interactions, the subordinate species displayed these behaviours longer than the dominant species. With the exception of interactions *S. minutes*-*S. araneus* and *S. araneus*-*N. anomalus* in the phase II, all differences were significant in both phases (Mann-Whitney *U*-test: U = 22.0 to 0.0, p = 0.033 to 0.0002). Moreover, the smaller the species, the longer the duration of active avoidance. Active avoidance was very rare in the dominating *N. fodiens* and the most frequent in *S. minutus*. In *N. anomalus* it was only observed in interactions with *N. fodiens* (Fig. 6).

The analysis of correlation demonstrated that the longer the distance between shrews, the shorter the conflict duration, especially in phase I (Fig. 7). For example, *N. fodiens* maintained long inter-individual distance and seldom took part in conflicts. In contrast, *N. anomalus* stayed close to its opponents and thus invested considerable time in conflicts. Duration of conflicts was positively correlated with the mobility of shrews. Again, the low mobility of *N. fodiens* coincided with the short duration of conflicts, and the high mobility of *N. anomalus* led to many conflicts. The correlation between mobility and duration of conflicts was stronger (significant) in phase II than I. There was no significant correlation between time of conflict and duration of stillness as well as active avoidance. In phase II of interactions, shrews exposed to many attacks from opponents displayed more active avoidance than the shrews rarely attacked. Decrease in duration of conflict (between phase I and II) was significantly dependent from reduction in mobility: the higher mobility reduction, the greater

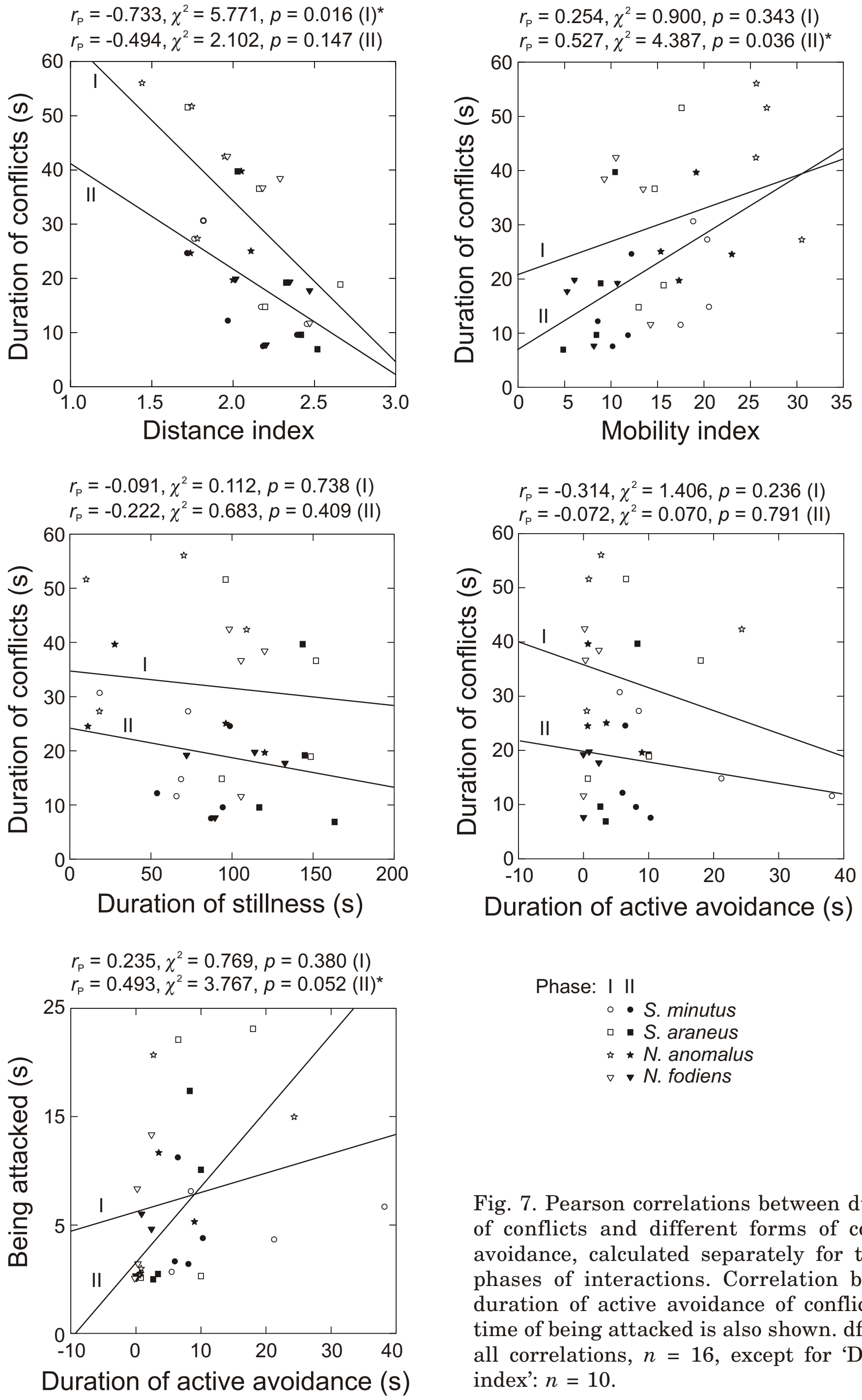

Fig. 7. Pearson correlations between duration of conflicts and different forms of conflicts avoidance, calculated separately for the two phases of interactions. Correlation between duration of active avoidance of conflicts and time of being attacked is also shown. df = 1 for all correlations, n = 16, except for 'Distance index': n = 10.

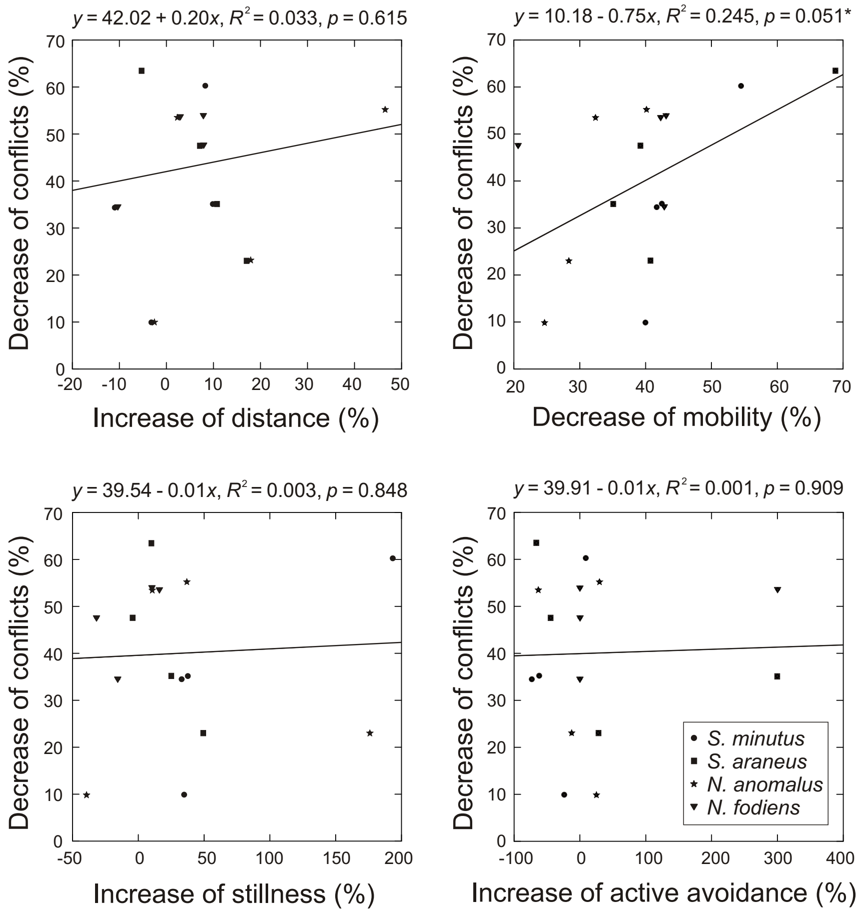

Fig. 8. Dependence of decrease of conflicts (between the two phases of tests) from changes in different forms of conflict avoidance. $n = 16$, except for 'Increase of distance': $n = 10$.

decrease in duration of conflict (Fig. 8). Decrease of conflict did not depend on increase of inter-individual distance, duration of stillness, nor duration of active avoidance.

Discussion

Consistent with our prediction, the duration of conflicts decreased with the passage of time of interactions. This decrease could result, at least partly, from mutual habituation of opponents to each other's presence. There is evidence that habituation functions as a mechanism to reduce aggression (Moynihan 1998, Langen *et al.* 2000, Bee and Gerhardt 2001). However, the observed differences among species and species combinations in the degree of conflict reduction, as well as in the other behaviours, indicates that other mechanisms contributed here besides habituation.

The decrease of conflicts was proportionally greater in intra- than interspecific interactions. This can be explained by the possibility that intraspecific social signals were better understood, and thus more effective, than interspecific ones. For example, threatening vocalisations differ among shrew species (Movchan and Shibkov 1982), and *N. fodiens* is able to distinguish threatening from submissive calls as well as intraspecific threats from those of *S. araneus* and synthesized call models (Movchan and Shibkov 1987).

Inter-individual distance correlated negatively with the time of conflicts, ie remaining at a long distance led to shorter duration of conflicts. However, we were not able to demonstrate that shrews additionally increased inter-individual distance (it did not change between phase I and II) and thus reduced duration of conflicts. One can impute that shrews did not boost the distance because they were not able go away further in our small terrarium. However, during the tests they did not stay at maximum possible distances: maximum value of distance index was 4, whereas the mean values observed ranged from 1.4 to 2.7. These results suggest that shrews do not avoid conflicts by increasing distance (ie retreating). On the other hand, retreats and escapes are perhaps the most common forms of avoiding conflicts in the wild. Foraging or exploring shrews emit ‘twitter’-calls almost continuously and it is believed that this vocalization helps them in mutual avoidance and usually prevents physical contacts (Crowcroft 1955, Gould 1969, Churchfeld 1990, L. Rychlik and R. Zwolak, pers. obser.). In the present study, however, retreats and escapes were included into ‘conflicts’ category because they occurred during or directly after a conflict.

N. fodiens maintained a long inter-individual distance and this correlated with a relatively short duration of conflicts. This result suggests that, consistent with our predictions, this large species effectively used this passive forms of conflict avoidance. However, it is possible that long inter-individual distances resulted also from the behaviour of the smaller opponents (evading *N. fodiens*) or the mutual avoidance. In contrast, *N. anomalus* tended to stay in a shorter inter-individual distance than the three other species. This can be a coincidental result of high mobility of *N. anomalus*.

Shrews’ mobility could be reduced, to some extent, by their diminishing motivation to escape or explore the terrarium, habituation to the stress of open field, fatigue, etc. But consistent with our prediction, the drop in mobility was usually stronger in animals submissive in a given trial. Moreover, the decrease in duration of conflict was dependent from reduction in mobility. This suggests that shrews indeed decreased their mobility to reduce duration of conflict. In contrast, in our previous analysis (Zwolak and Rychlik 2004), there was a negative (ie reversed) relationship between the decrease of mobility and the reduction of the number of conflicts. This inconsistency may result from different numbers of tested animals, but more important is the fact that previously we have analysed number, whereas now duration of conflicts. Seemingly, shrews reduced duration rather than number of conflicts.

Arranging the species from the most to the least mobile, in both phases the following order arose: *N. anomalus* > *S. minutus* > *S. araneus* > *N. fodiens*. The results obtained for the three latter species are consistent with our prediction: mobility (that should reflect the tendency to active forms of conflict avoidance) decreased with the increase of body size of shrews. But mobility was exceptionally high in *N. anomalus*. Similarly in Krushinska and Pucek's study (1989), mobility of *N. anomalus* was over two times higher than in *N. fodiens*, its decrease started few minutes later and it never decreased below that of *N. fodiens*. This phenomenon should be attributed to the higher sensitivity of *N. anomalus* to the stress of open field and unfamiliar surroundings (Michalak 1982, Krushinska and Pucek 1989, Krushinska and Rychlik 1993). This susceptibility can also explain the preferences of *N. anomalus* for habitat with dense plant cover (Andéra 1993, Rychlik 2000), decreased foraging efficiency in absence of cover (Rychlik 1997), and – most important in the context of this study – an increase in the number of conflicts in an unfamiliar open area (Krushinska and Rychlik 1993). Thus, the highest mobility and the most numerous conflicts observed in this study in *N. anomalus* were probably caused by a low resistance to the experimental conditions, rather than by its aggressiveness.

The obtained results suggest that stillness does not act as an effective mechanism reducing aggression and number of conflicts among shrews. However, with exception of *S. araneus*, the tendency to remain still increased with body size (*S. minutus* < *N. anomalus* < *N. fodiens*), which is consistent with our prediction. The stronger tendency to stillness was apparently related to greater energy reserves in the large water shrews. In contrast, due to the very small reserves of pygmy shrews (Hanski 1985), they could not stop foraging for a longer period. On the other hand, due to their small size, pygmy shrews are hard to perceive even when they move and it is easier for them to hide in crevices that are inaccessible for the larger species. Furthermore, predators prefer larger species of shrews as prey (Korpimäki and Norrdahl 1989). Thus, the risk of starvation exceeds the danger of being hunted by predators or attacked by another shrew and immobility was rare in *S. minutus*. The strong tendency of *S. araneus* to remain still can result from the fact that *S. araneus* is the most subfossorial (ie forages and stays in litter and upper layers of soils more than the other species – eg Churchfield 1991, Ellenbroek and Hamburger 1991). Open field and lack of litter or any cover could therefore present a stronger stress on this species, causing its stillness and low mobility.

In our study, only *S. araneus* and *N. fodiens* displayed freezing and there was high inter-individual variability in the duration of freezing and immobility. Duration of freezing did not change in any clear way with the passage of time. These results are surprising and hard to explain. Generally, a discrete and localizable threat source (as visible predator or opponent) promotes flight or defence, while an amorphous and difficult to locate threat source (as predator's or opponent's call or smell) promotes freezing or immobility (Blanchard *et al.* 1991). However, animals exposed to proximal, inescapable threats or attacks exhibit immobility and freeze, whereas they react by avoidance and flight to distant threats (Rodgers 1997, Dixon 1998). Their reaction can also be explained by access to shelter: they flee to a shelter or freeze if shelter is not available (Blanchard and Blanchard 1989).

Freezing or immobility were commonly observed reactions of rodents to different life threats as predation risk (eg Jędrzejewski *et al.* 1993, Hendrie *et al.* 1998, Eilam *et al.* 1999) or social pressure (eg Hendrie and Starkey 1998, Bauer and Gariepy 2001, Peres and Leite 2002), and tendency to such reactions increased with the strength of fear. Under the same conditions and stimuli, some rodent species display freeze, whereas other do not (Randal *et al.* 1995, Eilam *et al.* 1999). But even within a given species, some individuals freeze and other animals flee in reaction to the same stimulus (Hendrie and Starkey 1998, Edut and Eilam 2004), which is similar to our results.

In rodent social conflicts, losers showed usually increased immobility and lower locomotor activity (Lumley *et al.* 2000, Peres and Leite 2002). Reactions of our shrews seem to be opposite. The dominant *N. fodiens* exhibited lower mobility and more stillness than the submissive species. It also froze in contrast to *S. minutus* and *N. anomalus*. Similarly, Krushinska and Pucek (1989) observed that frequency and duration of freezing was much higher in *N. fodiens* than *N. anomalus*. According to Crowcroft (1955), common shrews begin to freeze as they become familiar with the cage. This suggests different functions of this behaviour in shrews and rodents. Lack of freezing can be related to extreme high energy requirements and an almost constant need for food searching in *S. minutus*, and high sensitivity to the stress of open field and unknown surrounding in *N. anomalus*.

All species displayed active forms of conflict avoidance (keeping distance and to-and-fro behaviours) and durations of these behaviours were similar in intraspecific interactions. This indicates that active avoidance is not species--specific and even large *Neomys* species possess these behaviours in their repertoire. However, interspecific interactions showed that duration of these behaviours decreased with the increase of body size of shrews. Moreover, the subordinate species displayed these behaviours much more frequently than the dominant species. These results are therefore consistent with our prediction that active forms of conflict avoidance are more important for small and subordinate species.

Reduction in the duration of conflicts did not depend on the increase of total time of active avoidance. But shrews exposed to many attacks displayed more active avoidance than the shrews rarely attacked. Since this relationship was significant in the later phase of interactions, we believe that this was the shrews' reaction, ie that shrews used active avoidance as a mechanism of conflict avoidance.

Arranging the species in accordance to the duration of active avoidance, gave us an order consistent with the domination hierarchy (L. Rychlik and R. Zwolak, in prep.): from *S. minutus* (the lowest position in the hierarchy and the longest duration of active avoidance), through *S. araneus*, *N. anomalus*, to *N. fodiens* (dominant species with the shortest active avoidance). The shortest duration of interspecific conflicts in *S. minutus* suggests that either other species did not perceive it as an important competitor or, more probably, *S. minutus* avoided aggression more efficiently than other species through high mobility and active avoidance behaviours. The avoidance was less effective only with *N. anomalus* because this species was so mobile that occasions to meetings and conflicts were frequent. Similarly to previous studies (Crowcroft 1955, Dickman 1991, Kalinin *et al.* 1998), *S. minutus* tried to retreat immediately after meeting another shrew, regardless of the species. Other species rarely withdrew before it came to threats or fight. Such conflicts, even if restricted to agonistic vocalisations, are connected with loss of energy and time that could be spent on foraging. Furthermore, when fighting occurs, it increases additional risk of injuries (Moynihan 1998). Considering that tested shrews frequently engaged in conflicts, the statement on minimal costs that dominating species incur due to interference (Dickman 1991), can be unconditionally accepted only in the case of interactions with pygmy shrews.

Dickman (1991) suggested that *S. minutus* might avoid larger shrew species because it can be regarded as a prey and attacked. He also pointed out that size and movements of pygmy shrews can resemble large insects that often fall victim to *S. araneus*. Nevertheless, in our trials we did not observe that larger shrew species tried to prey upon *S. minutus*.

Conclusions

(1) All shrew species (both subordinate and dominant) tended to reduce frequency and duration of conflicts with their opponents.

(2) The repertoire of mechanisms leading to conflict avoidance was not species-specific: it was not different or wider in small species (*S. minutus*, *S. araneus*) than in large ones (*N. fodiens*, *N. anomalus*). The displayed forms and efficiency of conflict avoidance depended rather on the dominance status of an animal in a given interaction.

(3) In contrast to small rodents, none of the tested shrew species avoided conflicts by the most passive forms: freeze and stillness reactions. The other forms (habituation, remaining in a long inter-individual distance, reduction of mobility, keeping distance behaviour, and to-and-fro behaviour) were used with a higher or lower efficiency by all species.

(4) Consistently with our predictions, large shrews (as *N. fodiens*) used the passive mechanisms of conflict avoidance (maintaining a long inter-individual distance and reduction of mobility), ie they tended to use the ‘wait-and-see’ strategy. In contrast, small shrews (as *S. minutus*) invested proportionally more time in active forms of aggression avoidance and thus tended to use the ‘escape’ strategy.

Acknowledgements: We are very grateful to A. Arasim, M. Babski, K. Bochowicz, I. Smerczyński and E. Sorato for their field and technician assistance, and to the three reviewers for their useful comments on our manuscript. Eunice Blavascunas kindly improved our English. This study was supported by grant no. 6 P04F 036 21 from the Committee for Scientific Research and by budgets of the Mammal Research Institute PAS and Adam Mickiewicz University.

References

Andéra M. 1993. Distribution of the Miller's water shrew *Neomys anomalus* in Czechoslovakia. Folia Musei Rerum Naturalium Bohemiae Occidentalis, Zoologica 37: 1–37.

Archer J. 1988. The behavioural biology of aggression. Cambridge University Press, Cambridge: 1–257.

Bauer D. J. and Gariepy J. L. 2001. The functions of freezing in the social interactions of juvenile high- and low-aggressive mice. Aggressive Behavior 27: 463–475.

Baxter R. M. and Irwin D. 1995. A laboratory study of agonistic behaviour in the red musk shrew, *Crocidura flavescens* (Geoffroy I. 1827). Zeitschrift für Säugetierkunde 60: 193–205.

Bee M. A. and Gerhardt H. C. 2001. Habituation as a mechanism of reduced aggression between neighboring territorial male bullfrogs (*Rana catesbeiana*). Journal of Comparative Psychology 115: 68–82.

Blanchard R. J. and Blanchard D. C. 1989. Antipredator defensive behaviors in a visible burrow system. Journal of Comparative Psychology 103: 70–82.

Blanchard D. C., Blanchard R. J. and Rogers R. J. 1991. Risk assessment and animal models of anxiety. [In: Animal models in psychopharmacology. B. Olivier and J. Slangen, eds]. Birkhäuser Verlag, Basel: 117–134.

Blaustein A. R. and Risser A. C. J. 1976. Interspecific interactions between three sympatric species of Kangaroo rats (*Dipodomys*). Animal Behaviour 24: 381–385.

Cantoni D., Favre L., Tencalla F., Croset P., Morgenthaler F., Camarda G., Ruchet C., Rivier L. and Vogel P. 1996. Intra- and inter-individual variation in flank gland secretions of free-ranging shrews *Crocidura russula*. Journal of Chemical Ecology 22: 1669–1688.

Churchfield S. 1984. Dietary separation in three species of shrew inhabiting water-cress beds. Journal of Zoology, London 204: 211–228.

Churchfield S. 1990. The natural history of shrews. Christopher Helm (Publishers) Ltd., Bromley: 1–178.

Churchfield S. 1991. Niche dynamics, food resources, and feeding strategies in multispecies communities of shrews. [In: The biology of the Soricidae. J. S. Findley and T. L. Yates, eds]. Special Publication of the Museum of Southwestern Biology, University of New Mexico, Albuquerque: 23–34.

Churchfield S., Nesterenko V. A. and Shvarts E. A. 1999. Food niche overlap and ecological separation amongst six species of coexisting forest shrews (Insectivora : Soricidae) in the Russian Far East. Journal of Zoology, London 248: 349–359.

Churchfield S. and Rychlik L. (in press). Dietary overlap and niche partitioning in four shrew species co-existing in marshland in Białowieża Forest, eastern Poland. Journal od Zoology, London.

Croin Michielsen N. 1966. Intraspecific and interspecific competition in the shrews *Sorex araneus* L. and *S. minutus* L. Archives Néerlandaises de Zoologie 17: 73–174.

Crowcroft W. P. 1955. Notes on the behaviour of shrews. Behaviour 8: 63–80.

Dempster E. R and Perrin M. R. 1990. Interspecific aggression in sympatric *Gerbillurus* species. Zeitschrift für Säugetierkunde 55: 392–398.

Dickman C. R. 1991. Mechanisms of competition among insectivorous mammals. Oecologia 85: 464–471.

Dixon A. K. 1998. Ethological strategies for defence in animals and humans: their role in some psychiatric disorders. British Journal of Medical Psychology 71: 417–445.

Eccard J. A. and Ylönen H. 2002. Direct interference or indirect exploitation? An experimental study of fitness costs of interspecific competition in voles. Oikos 99: 580–590.

Eccard J. A. and Ylönen H. 2003. Interspecific competition in small rodents: from populations to individuals. Evolutionary Ecology 17: 423–440.

Edut S. and Eilam D. 2004. Protean behavior under barn-owl attack: voles alternate between freezing and fleeing and spiny mice flee in alternating patterns. Behavioural Brain Research 155: 207–216.

Eilam D., Dayan T., Ben-Eliyahu S., Schulman I., Shefer G. and Hendrie C. A. 1999. Differential behavioural and hormonal responses of voles and spiny mice to owl calls. Animal Behaviour 58: 1085–1093.

Ellenbroek F. J. M. and Hamburger J. 1991. Interspecific interactions between the shrews *Sorex araneus* L. and *S. minutus* L. (Soricidae, Insectivora) and the use of habitat – a laboratory study. Netherlands Journal of Zoology 41: 32–61.

Enquist M. and Leimar O. 1990. The evolution of fatal fighting. Animal Behaviour 39: 1–9.

Feldhamer G. A., Drickamer L. C., Vessey S. H. and Merritt J. F. 1999. Mammalogy: adaptation, diversity, and ecology. WBC/McGraw-Hill, Boston: 1–563.

Frye R. J. 1983. Experimental field evidence of interspecific aggression between two species of kangaroo rat (*Dipodomys*). Oecologia 59: 74–78.

Gliwicz J. and Taylor J. R. E. 2002. Comparing life histories of shrews and rodents. Acta Theriologica 47, Suppl. 1: 185–208.

Gould E. 1969. Communication in three genera of shrews (Soricidae): *Suncus*, *Blarina* and *Cryptotis*. Communications in Behavioral Biology, Part A 3: 11–31.

Grant P. R. 1970. Experimental studies of competitive interaction in two-species system. II. The behaviour of *Microtus*, *Peromyscus* and *Clethrionomys* species. Animal Behaviour 18: 411–426.

Grant P. R. 1972. Interspecific competition among rodents. V. Summary of the evidence for rodent species, and some generalisations. Annual Review of Ecology and Systematics 3: 79–106.

Hanski I. 1985. What does a shrew do in an energy crisis? [In: Behavioural ecology. Ecological consequences of adaptive behaviour. The 25th Symposium of the British Ecological Society, Reading 1984. R. M. Sibly and R. H. Smith, eds]. Blackwell Scientific Publications, Oxford: 247–252.

Hanski I. 1994. Population biological consequences of body size in *Sorex*. [In: Advances in the biology of shrews. J. F. Merritt, G. L. Kirkland Jr and R. K. Rose, eds]. Special Publication of Carnegie Museum of Natural History, Pittsburgh 18: 15–26.

Harper S. J. and Batzli G. O. 1997. Are staged dyadic encounters useful for studying aggressive behaviour of arvicoline rodents? Canadian Journal of Zoology 75: 1051–1058.

Hawes M. L. 1976. Odor as a possible isolating mechanism in sympatric species of shrews (*Sorex vagrans* and *Sorex obscurus*). Journal of Mammalogy 57: 404–406.

Hawes M. L. 1977. Home range, territoriality and ecological separation in sympatric shrews *Sorex vagrans* and *Sorex obscurus*. Journal of Mammalogy 58: 354–367.

Hendrie C. A. and Starkey N. J. 1998. Pair-bond disruption in Mongolian gerbils: Effects on subsequent social behaviour. Physiology & Behavior 63: 895–901.

Hendrie C. A., Weiss S. M. and Eilam D. 1998. Behavioral response of wild rodents to the calls of an owl: a comparative study. Journal of Zoology, London 245: 439–446.

Jędrzejewski W., Rychlik L. and Jędrzejewska B. 1993. Responses of bank voles to odours of seven species of predators: experimental data and their relevance to natural predator-vole relationships. Oikos 68: 251–257.

Johannesen E., Brudevoll J., Jenstad M., Korslund L. and Kristoffersen S. 2002. Behavioural dominance of grey-sided voles over bank voles in dyadic encounters. Annales Zoologici Fennici 39: 43–47.

Kalinin A. A., Shchipanov N. A. and Demidova T. B. 1998. Behaviour of four species of shrews *Sorex isodon*, *S. araneus*, *S. caecutiens*, and *S. minutus* (Insectivora, Soricidae) in interspecific contacts. Zoologicheskii Zhurnal 77: 838–849. [In Russian with English summary]

Kirkland G. L. Jr 1985. Small mammal communities in temperate North American forests. Australian Mammalogy 8: 137–144.

Kirkland G. L. Jr 1991. Competition and coexistence in shrews (Insectivora: Soricidae). [In: The biology of the Soricidae. J. S. Findley and T. L. Yates, eds]. Special Publication of the Museum of Southwestern Biology, University of New Mexico, Albuquerque: 15–22.

Korpimäki E. and Norrdahl K. 1989. Avian and mammalian predators of shrews in Europe: regional differences, between-year and seasonal variation, and mortality due to predation. Annales Zoologici Fennici 26: 389–400.

Krushinska N. L. and Pucek Z. 1989. Ethological study of sympatric species of European water shrews. Acta Theriologica 34: 269–285.

Krushinska N. L. and Rychlik L. 1993. Intra- and interspecific antagonistic behaviour in two sympatric species of water shrews: *Neomys fodiens* and *N. anomalus*. Journal of Ethology 11: 11–21.

Krushinska N. L., Rychlik L. and Pucek Z. 1994. Agonistic interactions between resident and immigrant sympatric water shrews: *Neomys fodiens* and *N. anomalus*. Acta Theriologica 39: 227–247.

Langen T. A., Tripet F. and Nonacs P. 2000. The red and the black: habituation and the dear-enemy phenomenon in two desert Pheidole ants. Behavioral Ecology and Sociobiology 48: 285–292.

Law R., Marrow P. and Dieckman U. 1997. On evolution under asymmetric competition. Evolutionary Ecology 11: 485–501.

Lumley L. A., Charles R. F., Charles R. C., Hebert M. A., Morton D. M. and Meyerhoff J. L. 2000. Effects of social defeat and of diazepam on behavior in a resident-intruder test in male DBA/2 mice. Pharmacology Biochemistry and Behavior 67: 433–447.

Martin I. G. 1980. An ethogram of captive *Blarina brevicauda*. American Midland Naturalist 104: 290–294.

Maynard Smith J. and Parker G. A. 1976. The logic of asymmetric contests. Animal Behaviour 24: 159–175.

McNab B. K. 1991. The energy expenditure of shrews. [In: The biology of the Soricidae. J. S. Findley and T. L. Yates, eds]. Special Publication of the Museum of Southwestern Biology, University of New Mexico, Albuquerque: 35–45.

Michalak I. 1982. Reproduction, maternal and social behaviour of Mediterranean water shrew under laboratory conditions. Säugetierkundliche Mitteilungen 30: 307–310.

Movchan V. N. and Shibkov A. A. 1981. [On the significance of some acoustic signals in the behaviour of insectivores]. Vestnik Leningradskogo Universiteta 1981(2): 73–76. [In Russian with English summary]

Movchan V. N. and Shibkov A. A. 1982. Structural patterns of acoustic signals in shrews (Soricidae). Zoologicheskii Zhurnal 61: 1695–1705. [In Russian with English summary]

Movchan V. N. and Shibkov A. A. 1987. Recognition by shrews of the intraspecific communicational signals and their synthetised models. Vestnik Leningradskogo Universiteta Ser. 3, 1: 57–64. [In Russian with English summary]

Moynihan M. 1998. The social regulation of competition and aggression in animals. Smithsonian Institution Press, Washington: 1–158.

Nevo E., Naftali G. and Guttman R. 1975. Aggression patterns and speciation. Proceedings of the National Academy of Sciences of the USA 72: 3250–3254.

Olsen R. W. 1969. Agonistic behavior of the short-tailed shrew (*Blarina brevicauda*). Journal of Mammalogy 50: 494–500.

Platt W. J. 1976. The social organisation and teritoriality of short-tailed shrew (*Blarina brevicauda*) population in old field habitats. Animal Behaviour 24: 305–318.

Peres R. C. and Leite J. R. 2002. The influence of competitive status (winner/loser) on the behavior of male rats in three models of anxiety. Aggressive Behavior 28: 164–171.

Perri L. M. and Randall J. A. 1999. Behavioral mechanisms of coexistence in sympatric species of desert rodents, *Dipodomys ordii* and *D-merriami*. Journal of Mammalogy 80: 1297–1310.

Persson L. 1985. Asymmetrical competition: are larger animals competitively superior? The American Naturalist 126: 261–266.

Poduschka W. 1977. Insectivore communication. [In: How animals communicate. T. A. Seboek, ed]. Indiana University Press, Bloomington: 600–633.

Randall J. A., Hatch S. M. and Hekkala E. R. 1995. Interspecific variation in anti-predator behavior in sympatric species of kangaroo rat. Behavioral Ecology and Sociobiology 36: 243–250.

Rodgers R. J. 1997. Animal models of ‘anxiety’: where next? Behavioural Pharmacology 8: 477–496.

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

Rychlik L. 1998. Evolution of social systems in shrews. [In: Evolution of shrews. J. M. Wójcik and M. Wolsan, eds]. Mammal Research Institute, Białowieża: 347–406.

Rychlik L. 2000. Habitat preferences of four sympatric species of shrews. Acta Theriologica 45, Suppl. 1: 173–190.

Rychlik L. 2001. Habitat preferences of water shrews and root vole coexisting along a stream in Białowieża Forest. Säugetierkundliche Informationen 5 (25): 99–112.

Rychlik L. 2005. Overlap of temporal niches among four sympatric species of shrews. Acta Theriologica 50: 175–188.

Rychlik L. and Jancewicz E. 1998. Prey preferences and foraging behaviour in semi-aquatic and terrestrial shrews – cafeteria test. [In: Abstracts of the Euro-American Mammal Congress, Santiago de Compostela, Spain, 19–24 July, 1998. S. Reig, ed]. Universidade de Santiago de Compostela, Santiago de Compostela: 186.

Rychlik L. and Jancewicz E. 2002. Prey size, prey nutrition, and food handling by shrews of different body sizes. Behavioral Ecology 13: 216–223.

Schoener T. W. 1983. Field experiments on interspecific competition. The American Naturalist 122: 240–285.

Schröpfer R. 1990. The structure of European small mammal communities. Zoologische Jahrbücher. Systematik, Ökologie und Geographie der Tiere 117: 355–367.

Shchipanov N. A., Kalinin A. A., Oleinichenko V. Yu. and Demidova T. B. 1998. General behavioral characteristics of shrews. Russian Journal of Zoology 2: 300–312.

Shchipanov N. A. and Oleinichenko V. Yu. 1993. [The bicoloured white-toothed shrew. The behaviour and spatial, ethological and functional structure of a population]. Nauka, Moskva: 1–136. [In Russian]

Sheftel B. I. and Hanski I. 2002. Species richness, relative abundances and habitat use in local assemblages of *Sorex* shrews in Eurasian boreal forests. Acta Theriologica 47, Suppl. 1: 69–79.

Sokal R. R. and Rohlf F. J. 1995. Biometry. The principles and practice of statistics in biological research. W. H. Freeman and Company, New York: 1–859.

Taylor J. R. E. 1998. Evolution of energetic strategies in shrews. [In: Evolution of shrews. J. Wójcik M. and M. Wolsan, eds]. Mammal Research Institute, Polish Academy of Sciences, Białowieża: 309–346.

Vogel P. 1976. Energy consumption of European and African shrews. Acta Theriologica 21: 195–206.

Wolff J. O. and Dueser R. D. 1986. Noncompetitive coexistence between *Peromyscus* species and *Clethrionomys gapperi*. Canadian Field Naturalist 100: 186–191.

Young K. A. 2003. Evolution of fighting behavior under asymmetric competition: an experimental test with juvenile salmonids. Behavioral Ecology 14: 127–134.

Zwolak R. and Rychlik L. 2004. Does the reduction of locomotor activity serve as an aggression avoidance mechanism in shrews (Soricidae)? Electronic Journal of Polish Agricultural Universities, Biology 7(2) http://www.ejpau.media.pl/series/volume7/issue2/biology/art-06.html.

Received 21 April 2005, accepted 25 July 2005.

Associate Editor was Krzysztof Schmidt.