Interspecific aggression and behavioural dominance among four sympatric species of shrews

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Abstract: Level of interspecific aggressiveness should reflect intensity of interference competition, and large-dominant and small-subordinate species should evolve aggressive and passive agonistic behaviours, respectively, to achieve stable co-existence. We tested these ideas investigating interspecific behavioural dominance in a four-species community of shrews differing in body size (*Sorex minutus* Linnaeus, 1766; *Sorex araneus* Linnaeus, 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 '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 least pronounced dominance of *N. anomalus* over *S. araneus* suggest the strongest interference competition 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, dominating species restricted the access of subordinate species to the shelter.

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 a similar way (Root 1967). So far, most research on competition in small mammals concerned rodents and focused on the influence of exploitation competition on microhabitat selection or population dynamics (Eccard and Ylönen 2002, 2003). There are much less studies on interference competition (Eccard and Ylönen 2002) and in general, much less is known on competition among shrews (Kirkland 1991).

Interference competition occurs when some individuals directly (e.g. by fighting) reduce the access of other individuals to the 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 both 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 non-competitive co-existence (e.g. Wolff and Dueser 1986; Perri and Randall 1999). Usually, (1) aggression is higher between sympatric and closely related species than between allopatric and unrelated ones (Nevo et al. 1975; Dempster and Perrin 1990), (2) ecological 'specialist' species dominate 'generalists' (Blaustein and Risser 1976; Ambrose and Meehan 1977; Dempster and Perrin 1990), and (3) larger species dominate smaller species (Ambrose and Meehan 1977; Frye 1983; Schoener 1983; Johannesen et al. 2002; Langkilde and Shine 2004). However, the dominance of smaller species over larger ones has been also observed (e.g. Miller and 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 evolve 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 or vocalizations). Interspecific aggression, dominance and territoriality are advantageous because they reduce competition for resources and risk of injury, and saves 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.

Soricinae shrews seem to be an excellent model to investigate competition because: (1) they usually coexist in multi-species communities (Kirkland 1991; e.g. nine species in central Siberia – Churchfield and Sheftel 1994); (2) their metabolic rates and food requirements are the highest among mammals (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 (Churchfield 1990; Hanski 1994; Gliwicz and Taylor 2002). All this requires from them particularly effective mechanisms of resource partitioning. An advantage of small body size of shrews is that more species can coexist in a given habitat (Kirkland 1991). However, relatively large body size conveys a competitive advantage to the members of a shrew community, because it facilitates access to higher-quality foraging microhabitats (Fox and Kirkland 1992).

In the wet habitats of Białowieża Forest (eastern Poland) co-exist four species of Soricinae shrews: pygmy shrew *Sorex minutus* Linnaeus, 1766, common shrew *Sorex araneus* Linnaeus, 1758, Mediterranean water shrew *Neomys anomalus* Cabrera, 1907, and Eurasian water shrew *Neomys fodiens* (Pennant, 1771). They form a guild (Schröpfer 1990), so intra- and interspecific 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 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 enabling 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 differ in body size, we expected that this factor will 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 Soricinae shrews, which are strictly territorial and solitary, *N. anomalus* shows considerable level of intraspecific tolerance and supposedly is more gregarious (Krushinska and Rychlik 1993; Krushinska et al. 1994; Rychlik 1998). Thus, one can expect that *N. anomalus* will differ in aggressive behaviour from the other studied species. Previous studies (Krushinska and Pucek 1989; Krushinska and Rychlik 1993; Krushinska et al. 1994) showed that both species of water shrews displayed many conflicts near food and, especially, shelters. Thus, we also attempted to determine if the competition for food or shelter changes 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) 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 are influenced by the social organization of a given species; (4) competition for resources (as food or shelter) increases intra- and interspecific aggressiveness; and (5) dominating species restrict the access of subordinate species to resources. In consequence, we tested the following predictions: (1) aggressiveness and dominance rank will be the higher in larger species of shrews; (2) large-dominant and small-subordinate species will display mainly aggressive and passive agonistic behaviours, respectively; (3) aggressiveness and dominance rank of the gregarious *N. anomalus* will be lower than expected according to its body size; (4) the presence of food or shelter will increase the intra- and interspecific aggressiveness and conflicts; and (5) dominating species of shrews will spend more time by 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 (E Poland) between June

and September of 2000-2002. Pitfalls, containing a handful of moss as bedding, a tea-spoon of minced beef as bait/food and covered with a roof protecting from rain, were used for live-trapping. The traps were opened in afternoon (usually about 1700 hrs), checked every 2-2.5 hours, and closed usually about midnight. Trapping was not performed during heavy rain-falls and cold evenings. Animals were transported to the laboratory in buckets containing moss bedding and food (minced beef and/or fly larvae). Transportation lasted 10-20 minutes. In the laboratory shrews were placed in individual cages ($30 \times 40 \times 15$ cm), where they acclimatized 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 lib. 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 in captivity 1-8 weeks, 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 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 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 neutral arena remain scarce (e.g. Krushinska and Pucek 1989; Kalinin et al. 1998).

A total of 69 subadult animals (i.e. young-of-the-year, fully grown but sexually immature) were used in dyadic encounters: 17 individuals of *S. minutus*, 19 of *S. araneus*, 15 of *N. anomalus*, and 18 of *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 few succeeding years, such episodes were probably rare. It was impossible to sex these animals and perform one-sex dyads, but social behaviour of subadult males and females is similar (Rychlik 1998). Animals were tested in a

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separate room during daytime, usually between 09:00 and 16:00 hours, i.e. during the period of partly decreased activity of shrews (Rychlik 2005). To ensure that the tested animals were not satiated, feeding trays were removed from their cages approximately one hour before the experiment. A pair of animals was placed in neutral arena, that is a bare glass terrarium measuring $70 \times 30 \times 40$ cm (Fig. 1), and their behaviour was video-recorded. 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 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. In the first part ("separated", duration 5 minutes), the animals stayed on the different halves of the terrarium, separated by a transparent plastic partition (Fig. 1). During this stage, shrews could settle in after removal from individual cages and explore the new surroundings without the physical contact with the second individual. In other studies, this period was similar: 3-5 minutes (eg Cranford and Derting 1983; Krushinska and Pucek 1989; Dempster and Perrin 1990; Harper and Batzli 1997). In the second part ("open field", duration 5 minutes), the partition was removed and the animals could begin to interact in so-called "neutral open field". In the third part ("food", duration 10 minutes) a bowl with minced meat was placed in the terrarium in order to elicit competition for food. In the fourth stage ("shelter", duration 10 minutes), the bowl was replaced with a reversed pot that served as a shelter (Fig. 1). Since most soricine shrews are unable to utilize resources communally (Rychlik 1998), introduction of only one bowl and one shelter resulted in short supply of resources. Previously, Krushinska and Pucek (1989) placed two water shrews for 5 minutes in separated halves of an arena, and then tested them for 30 minutes in open field plus next 30 minutes after placement of a shelter (65 minutes in total). To avoid prolonged aggressive encounters, we have shortened duration of our tests to 30 minutes. For comparison, recently agonistic interactions among shrews were usually tested in open field for 10-12 minutes (Baxter and Irwin 1995; Kalinin et al. 1998; Shchipanov et al. 1998; Oleinichenko 2000).

Immediately after the trials, animals were weighted with the 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 60 interspecific trials were conducted and the number of tests per each pair of species is presented in Table 1. It was impossible to capture enough shrews to use each of them only once. Thus, each individual took part in 1-4 (mostly 2) tests, but each time with a different species (in a random order). The only exceptions were made by the participation of one *N. anomalus* 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 from these two trials for describing the behaviour of *N. anomalus* and *S. minutus* respectively, 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 that apparently reduced the carry-over effect of loss or victory in a prior trial.

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, we have followed the mentioned authors and classified the observed behaviour of shrews as:

1) Non-agonistic – divided to: (a) amicable (or integrative) – "naso-anal whirling" (intensive reciprocal sniffing when two shrews remained in close contact, almost "interwoven"), crawling on each other, and going around; (b) neutral (or identification) – approaching the other animal and sniffing it from some distance; (c) contact avoidance (or rejection) – "keeping distance behaviour" (avoiding adversary by simultaneous movements in more or less constant distance from the other), "to-and-fro behaviour" (approaching the animal followed by quick withdrawal), and "freeze" (motionless except vibrissae and snout); (d) marking – dragging the anogenital area against the terrarium floor.

2) Agonistic – divided to: (a) offensive behaviours – including 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, in close distance), and follow (slower, in some distance); (b) defensive behaviours – comprising retreating, jumping away and escaping (i.e. running away), all as a result of direct contact; (c) threats – including stance, tripedal, sideways, back and upright postures, and threatening vocalization (it occurred with almost each conflict, regardless if it came to fight or the animals stopped at threats). Vocalizations were not

analyzed because the identification of a vocalizing individual in interacting pair was unreliable.

3) Resource use – divided to: (a) food utilization – eating and sniffing food, remaining in tactile contact with bowl with food; (b) shelter occupation – staying inside the shelter or protruding from its entrance.

4) Other (not analyzed in the present paper) – included exploration (walking, running, sniffing, jumping on terrarium walls or nest box, digging attempts), attentive (active but remaining in a place), resting, self-grooming, and defecation/urination.

Determination of dominance hierarchy

Behavioural dominance and subordination are defined here not as social ranks of individuals within a group of conspecifics, but as a position of species in competitive interactions within a community of species. We assumed that averaging results of interactions between individuals of different species we will be able to determine dominance of one species over another. We compared mean total times of offensive and defensive behaviours displayed by particular shrew species during 5 minutes. These behaviours occurred usually in long (often consecutive) bouts, which could not be divided into single acts. Therefore, we used the measure of total duration (and not mean number) of acts per unit of time. Similarly to 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 species, which attacked more and escaped less often, was dominating in a given interaction. Additional measures of dominance were: total time spent by food, total time spent in shelter, and shelter residence during last minute of the test. We assumed that dominating shrews will spend longer times by food and in shelter, as well as they will be the last occupants of the shelter.

Threats occurred in both offensive and defensive contexts, hence we did not consider this behaviour as a direct measure of the dominance. Nevertheless, we assumed that the level of threatening indicates intensity of the conflicts, and suggests its equivocal outcome (i.e. the more threats in interactions of a given pair of animals/species, the less definitive dominance of one individual/species over another). To investigate the effects of competition for resources on dominance hierarchy, we compared the duration of offensive and defensive behaviours in consecutive

stages of the trials: "open field", "food" and "shelter".

Data analysis

Duration of a single behavioural act was measured with the accuracy of 1 second. The durations of particular categories of behaviour were summed separately for each stage of the test and expressed as "total duration per 5 minutes". The results of all trials in a given pair of species were averaged and these means are presented on graphs along with standard errors. The mean durations of agonistic behaviours (offensive+defensive+threatening) were converted to percentages (with their sums being 100%) and presented in Fig. 2. In most statistical analyses, three steps were performed: (1) The 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 inter-combination 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 of the chance of Type1 Error, the conventional level of significance ($p < 0.05$) was adjusted by applying the False Discovery Rate procedure (Curran-Everett 2000) that has some advantages in comparison to the commonly used Bonferroni and other procedures. Following computer programs were used: Observer Video-Pro ver. 4.1, FoxPro ver. 2.5b, MS Excel '97, GraphPAD InStat ver. 1.13, and SYSTAT ver. 5.03.

Ethical note

The animals were cared for in accordance with the *Guidelines for the treatment of animals in behavioural research and teaching* (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 assumed that all conflicts, which pose a threat to the health of the animals, would be stopped. 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 shrews were released back in the wild. We have obtained permissions (no. DLOPiKog. 4201-206/00 of 17 July 2000 and no. DLOPiKog. 4201-04-136/2001/2002 of 28

February 2002) from the Minister of Environment for our capturing of the protected shrews and an acceptance (no. 2001/11 of 11 January 2001) from the Local Ethical Commission for Experiments with Animals in Białystok (Poland) for our experimental methods.

RESULTS

Interspecific differences in agonistic behaviour

S. minutus initiated especially many defensive interactions (significantly more than its three opponents: $G = 4.561$ to 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 that towards *S. araneus* and *N. anomalus* ($G = 13.161$ and 14.287 respectively, $p < 0.001$). *Sorex araneus* displayed significantly more threats and less offensive behaviours towards *N. anomalus* and *N. fodiens* than towards *S. minutus* ($G = 32.313$ and 31.231 respectively, $p < 0.001$ for threats; $G = 39.782$ and 31.474 respectively, $p < 0.001$ for attacks). *Neomys anomalus* displayed significantly more offensive behaviours towards the two *Sorex* species than towards *N. fodiens* ($G = 15.903$, $p < 0.001$ for *N. anomalus* towards *S. minutus* vs. *N. anomalus* towards *N. fodiens*; $G = 23.344$, $p < 0.001$ for *N. anomalus* towards *S. araneus* vs. *N. anomalus* towards *N. fodiens*), 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 were offensive behaviours and the longer threats displayed by *N. fodiens*: 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 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

Duration of offensive behaviours (Fig. 3) was very diversified among species combinations in all three stages of the tests (Kruskal-Wallis test: $H = 33.242$ to 82.684, $p = 0.000$, $df = 11$). In each combination of species and in all stages of the tests, individuals of larger species attacked longer and more frequently. After False Discovery Rate procedure (FDR), the differences were significant in 3 out of 6 interspecific combinations in the "open field" stage (Mann-Whitney *U*-test:

U = 2.0 to 11.5, p = 0.001 to 0.037), 5 combinations in the "food" stage (U = 1.0 to 27.5, p = 0.0003 to 0.018), and 1 combination in the "shelter" stage (U = 18.5, p = 0.018). *N. 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 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, ordering the species after the time of offensive behaviours, the following hierarchy resulted: *N. fodiens* (the highest position), *N. anomalus*, *S. araneus* and *S. minutus* (the lowest position). Comparing the level of interspecific aggressiveness, *Neomys* shrews were more aggressive than *Sorex* shrews. The duration of offensive behaviours initiated by *N. anomalus* towards *S. araneus* was particularly long (up to 22.1 s/5 min), and even in the "shelter" stage it remained at the high level (more than 5 s/5 min). The shortest total time of attacks (0-0.8 s/5 min) was recorded in *S. minutus* (Fig. 3).

Duration of defensive behaviours (Fig. 4) was also very diversified among species in all stages of the tests (Kruskal-Wallis test: H = 56.011 to 73.194, p = 0.000, df = 11). It was 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 to 24.5, p = 0.0002 to 0.017), with only the exception of interactions between *S. araneus* and *N. fodiens* in the "shelter" stage (U = 27.5, p = 0.094). Regardless of the stage, the defensive behaviours were shortest in *N. fodiens* (from 0.3 to 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* 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 as the one created according to the duration of attacks: *N. fodiens* (dominating), *N. anomalus*, *S. araneus*, and *S. minutus* (the lowest rank).

Also duration of threats (Fig. 5) significantly differed among species in all stages of the tests (Kruskal-Wallis test: H = 33.194 to 53.774, p = 0.000, df = 11). In most paired species, the smaller one tended to spend longer time threatening than the larger one. This could suggest that threats expressed defensive rather than offensive activity, and indicated a subordinate species in a given

combination. However, (1) in all test-stages none of two-species comparisons revealed a significant difference, (2) in a few cases the larger species invested similar or even longer time in threats (interactions *S. minutus-N. anomalus*, *S. minutus-N. fodiens*, and *N. anomalus-N. fodiens*), and (3) *S. minutus*, which theoretically should invest the longest time in defensive threats, spent usually shorter time on this activity than the other three species. Thus, it was not possible to order the four species into a dominance hierarchy based on the duration of threats.

On the other hand, threats were particularly long in interactions of *S. araneus* towards *N. anomalus*, i.e. between the two species most similar in body mass (31.7 s/5 min in "open field", 22.3 s/5 min in "food" and 10.9 s/5 min in "shelter" stages; Fig. 5). They were, for example, significantly longer than threats of *S. araneus* towards *S. minutus* in all test-stages (Mann-Whitney *U*-test: $U =$ 4.0 to 18.0, $p = 0.0003$ to 0.005, valid after FDR). Threats of *S. araneus* towards *N. anomalus* remained long even after introduction of a shelter into the terrarium. Similarly, the duration of threats showed by *N. fodiens* was the longest in interactions with the most similar in body size *N. anomalus*. In contrast, the shortest time of threats was recorded in interactions between *N. fodiens* and *S. minutus*. All this suggests that a short time of threats in interspecific interactions indicates big differences in dominance ranks, whereas a long time of threats means close or unclear positions of a given species in the hierarchy.

Competition for food and shelter

In opposition 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 "food" and "shelter" stages (Figs 3-5). Even if this reduction was not much pronounced 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 nearly to zero in the "shelter" stage.

As to offensive behaviours (Fig. 3), the reduction between "open field' and "food" stages was insignificant in all interactions, whereas between "food" and "shelter" stages it was significant in all six cases in which *Neomys* shrews initiated attacks (Kruskal-Wallis test: $H = 7.905$ to 13.731, $p = 0.019$ to 0.001, $df = 2$; Wilcoxon test: $Z = -2.366$ to -2.809, $p = 0.025$ to 0.005, valid after

FDR). In contrast, the duration of interspecific offensive behaviours initiated by the two *Sorex* species was so short in all test-stages that only one significant reduction was recorded: between "food" and "shelter" stages in interactions of *S. araneus* towards *S. minutus* ($Z = -2.375$, $p = 0.018$). 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 comparison "open field" vs. "food" stages but significant in 7 out of 12 cases in comparison "food" vs. "shelter" stages (Kruskal-Wallis test: $H = 6.316$ to 14.541, $p = 0.043$ to 0.001, $df = 2$; Wilcoxon test: $Z = -2.375$ to -2.938, $p = 0.018$ to 0.003, valid after FDR). Also in threatening time (Fig. 5), reduction was more pronounced between "food" and "shelter" than between "open field" and "food" stages, but no difference was significant after FDR adjustment.

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

Time spent in the shelter (Fig. 7a) differed among species as well (Kruskal-Wallis test: $H = 34.794$, $p = 0.000$, $df = 11$). The individual of the larger species always spent more time in the shelter than the smaller one (Fig. 7a). In 4 out of 6 interspecific combinations, the differences were significant (Mann-Whitney *U*-test: $U = 0.0$ to 16.0, $p = 0.001$ to 0.012). Similarly, the larger of the two tested species remained more frequently in the shelter during the last minute of a trial (Fig. 7b). After FDR procedure, the difference was significant only in 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 dominance order based on the occupation of shelter: *N. fodiens*, *N. anomalus*, *S. araneus*, and *S. minutus*.

DISCUSSION

Procedure and data set

Aggression between individuals of different species may be much more context dependent than can be recognized in laboratory experiments. When the individuals of each species are living in their normal niche environments, the repertoire of their responses in potential encounters may be broader than in this test situation. As an example, smaller species may take refuge from and avoid contact with larger species. However, experimental situations must be simplified to provide adequate control over investigated variables. In our tests, simplified environment was necessary to efficiently determine the order of behavioural dominance.

We tested most of our animals in more than one test. In contrast to laboratory mice or rats, wild shrews are available in limited numbers (especially *N. anomalus* and *S. minutus* are difficult to collect in Białowieża Forest). Therefore, we were forced to use some individuals a few times. However, they were never used two times in the same species-combination (with only three exceptions) and the consecutive tests of the same individual were separated by at least a 3-day break. On the other hand, the procedure of repeated tests of the same individuals was 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.

Under the unchanging sequence of test-stages ("separated", "open-field", "food" and "shelter"), aggressiveness of shrews, contrary to our prediction, decreased gradually from stage to stage. We considered random changing the sequence of stages in every test to separate out the effects of habituation and fatigue. However, we were concerned that: (1) such a procedure would increase the inter-individual variation in behaviour; (2) the tests with a different sequence of stages would not be fully comparable; (3) the presence of shelter at an early stage of test might determine and fix dominance of one shrew over another, so that their interactions in next stages would decline.

Nevertheless, we agree that our procedure could not verify undoubtedly if competition for food or shelter increases intra- and interspecific aggressiveness.

Indicators of behavioural dominance

Based on the results of this study, we can propose reliable and point out inadequate indicators of behavioural dominance in shrews. The dependable ones are: total time of attacks, total time of escapes, total time spent in shelter, and occupation of shelter at the end of a trial. Behavioural patterns called "keeping distance" and "to-and-fro", which typify subordinate individuals, also proved to be useful in analyses of dominance order (Rychlik and Zwolak 2005). In contrast, time spend by food and duration of threats proved to be inefficient indicators. The former seems to be influenced by different energetic requirements of studied species. Contrary to our prediction, the least *S. minutus* spent long time by 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 presence or rank of the competitor. On the other hand, large *N. fodiens* could not exhaust its body energy reserves during 30-minute-tests, thus they 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 these 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 common shrews interacting with water shrews) and dominant ones (e.g. *N. fodiens* tended to threat more often than *N. anomalus* in the "open field" stage). On the other hand, the total time of threats may help indicate which animals or species are of a similar rank in the dominance order. It was particularly high in the interactions of the two species most similar in body size, i.e. *S. araneus* and *N. anomalus*. Thus, this supports our assumption that animals/species with a similar strength threat each other more often than the animals/species with clearly separated positions in the dominance hierarchy.

Interspecific dominance

The dominance order determined with the use of 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 the position in the dominance hierarchy. This result corresponds also to former findings on 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; Ellenbroek and Hamburger 1991; Dickman 1988, 1991). However, in contrast to the mentioned studies, our study involved the entire shrew community and provided both qualitative and quantitative evidences, based on relatively large and credible data.

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

It was not surprising that dominating Eurasian water shrews were attacked only occasionally by smaller species. However, it was unexpected that pygmy shrews were also rarely attacked. There are two mutually non-exclusive explanations for this finding: (1) the position of *S. minutus* could be so low that conflicts ended with threats, and the bigger species did not have to recourse to an actual fight; and (2) *S. minutus* efficiently avoided direct contacts 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 especially numerous conflicts. Moreover, *S. araneus* occupied shelter at the end of trials only slightly less often than *N. anomalus* did. Such similarity of the positions in dominance hierarchy could 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 during conflicts (Maynard Smith and Parker 1976; Young 2003). On the other hand, our prediction that *N. anomalus* (as more social and thus potentially less aggressive and more tolerant) will take lower position in the dominance order than *S. araneus*, was not confirmed. Perhaps the higher than expected dominance rank of *N. anomalus* is a result of its stress-enhanced aggression. High excitability and susceptibility of *N. anomalus* to stress of unknown surroundings and open field have been previously reported (Michalak 1982; Krushinska and Pucek 1989; Krushinska and Rychlik 1993; Krushinska et al. 1994). Under such conditions, the aggressiveness and the number of conflicts initiated by *N. anomalus* increased, but dropped soon after those shrews acquainted themselves with the surroundings (Krushinska and Rychlik 1993; Krushinska et al. 1994) or immediately after shelters were offered (Krushinska and Pucek 1989). The same reactions (high 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 sizes of the interacting species are similar, domination and subordination may depend on the place of interaction rather than the species. In such instances, we are dealing with interspecific territoriality. For example, in interactions between two rodent species (*Peromyscus leucopus* and *P. maniculatus*), individuals that resided on their territory dominated (Wolff et al. 1983). The cases of interspecific territoriality are known also in the Soricidae family (e.g. *S. vagrans* and *S. ornatus* - Hawes 1977; *S. araneus* and *S. coronatus* - Neet 1989). The dominance hierarchy demonstrated in the present study is based on interactions in a place unfamiliar to both adversaries (neutral arena). Since *S. araneus* is intra- and interspecifically territorial (e.g. Croin Michielsen 1966; Neet 1989), we cannot rule out that in the wild, *S. araneus* dominate within their territories over *N. anomalus*.

Interference competition

Many studies showed that interspecific aggression among rodents reflected the interference competition that influenced 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, the interference competition is recognized as an important factor structuring the communities of shrews (Dickman 1991). He suggests that for the dominating species of shrew the

cost of interference is negligible, whereas the profit after securing exclusive access to the resources-rich microhabitat is high. For the subordinate species, the benefits from temporary use of the same rich microhabitat often exceed the costs of necessary vigilance and escapes to nearby refuge. However, the absence of a shrew species in a particular habitat may be caused by the interference competition with larger species (Hanski and Kaikusalo 1989). Neverteless, it can be accepted that the interference competition acts as one of the mechanisms shaping also the niches and fitness of shrew species coexisting in wet habitats of Białowieża Forest. And then, interspecific aggression may be an outcome of rather than a cause for the interspecific relations in a given community.

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

N. anomalus is probably subjected to a strong interference from both *N. fodiens* and *S. araneus*. In areas of allopatry, *N. anomalus* live 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 placed directly near water (Rychlik 2000, 2001). At the same time, in drier places *N. anomalus*

meets *S. araneus* that usually dominates numerically. We found that *N. anomalus* dominated behaviourally over *S. araneus*, but this supremacy is only slight and hard-fought. 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 the densities of *N. fodiens* and *S. araneus* (Dehnel 1950; Aulak 1970; Niethammer and Krapp 1990; Mitchell et al. 1999; Rychlik 2000 and unpubl.).

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 method 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, and not exploitation as the mechanism of competition. Currently, similar studies, but investigating the four-species community of shrews, have been conducted in Białowieża and the preliminary results suggest that interference competition indeed proceeds here 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 better answer the questions about importance and mechanisms of competition among Soricidae species.

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 (time of offensive and defensive behaviours, time spent in shelter) and unreliable (duration of threats, and time spent by food) indicators of interspecific dominance. As to the tested hypotheses and predictions: (1) Aggressiveness was higher in larger species, thus dominance rank seemed to be positively correlated with body size at specific level. (2) The larger *Neomys* species were more aggressive and initiated relatively more offensive behaviours, whereas the smaller *Sorex* species initiated more defensive behaviours. (3) Aggressiveness and dominance rank of

N. anomalus (the gregarious species) was not lower than expected according to its body size. So this study did not prove that aggressiveness and dominance rank are influenced by the social organization of a given species. (4) This study did also not show that competition for food or shelter increased interspecific aggressiveness. (5) However, individuals of dominating species spent more time in shelter than individuals of subordinate species. Thus, dominating species restricted the access of subordinate species to resources (shelter under these experimental conditions).

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REFERENCES

Ambrose, R.F., and Meehan, T.E. 1977. Aggressive behavior of *Perognathus parvus* and *Peromyscus maniculatus*. J. Mammal. **58**: 665-668.

Aulak, W. 1970. Small mammal communities of the Białowieża National Park. Acta Theriol. **15**: 465-515.

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

Blaustein, A.R., and Risser, A.C.J. 1976. Interspecific interactions between three sympatric species of Kangaroo rats (*Dipodomys*). Anim. Behav. **24**: 381-385.

Camargo, J.A. 1992. Can dominance influence stability in competitive interactions? Oikos, **64**: 605-610.

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

Churchfield S. & Rychlik L. (2006): Diets and coexistence in *Neomys* and *Sorex* shrews in Białowieża Forest, eastern Poland. Journal of Zoology, London. (in press)

Churchfield, S., and Sheftel B.I. 1994. Food niche overlap and ecological separation in a multi-species community of shrews in the Siberian taiga. J. Zool., Lond. **234**: 105-124.

Cihakova, J., and Frynta, D. 1996. Intraspecific and interspecific behavioural interactions in the wood mouse (*Apodemus sylvaticus*) and the yellow-necked mouse (*Apodemus flavicollis*) in a neutral cage. Folia Zool. **45**: 105-113.

Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am. Nat. **122**: 661-696.

Cranford, J.A., and Derting, T.L. 1983. Intra and interspecific behavior of *Microtus pennsylvanicus* and *Microtus pinetorum*. Behav. Ecol. Sociobiol. **13**: 7-11.

Croin Michielsen, N. 1966. Intraspecific and interspecific competition in the shrews *Sorex araneus* L. and *S. minutus* L. Arch. Neer.. Zool. **17**: 73-174.

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

Curran-Everett, D. 2000. Multiple comparisons: philosophies and illustrations. Am. J. Physiol.: Regul. Integ. Comp. Physiol. **279**: R1–R8.

Dehnel, A. 1950. Studies on the genus *Neomys* Kaup. Ann. Univ. Mariae Curie-Skłodowska, Sec. C **5**:1-63. [In Polish with Russian and English summaries]

Dempster, E.R., and Perrin, M.R. 1990. Interspecific aggression in sympatric *Gerbillurus* species. Z. Säugetierk. **55**: 392-398.

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

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

Downes, S., and Bauwens, D. 2002. An experimental demonstration of direct behavioural interference in two Mediterranean lacertid lizard species. Anim. Behav. **63**: 1037-1046.

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. Evol. Ecol. **17**: 423-440.

Ellenbroek, F.J.M. 1990. An experimental analysis of interspecific competition in the shrews *Sorex araneus* L. and *S. minutus* L. (Soricidae, Insectivora). PhD thesis, University of Leiden: Leiden.

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. Neth. J. Zool. **41**: 32-61.

Falkenberg, J.C., and Clarke, J.A. 1998. Microhabitat use of deermice: effects of interspecific interaction risks. J. Mammal. **79**: 558-565.

Feldhamer, G.A., Drickamer, L.C., Vessey, S.H., and Merrit, J.F. 1999. Mammalogy: adaptation,

diversity, and ecology. WBC/McGraw-Hill, Boston.

Fox, B.J., and Kirkland, G.L., Jr. 1992. An assembly rule for functional groups applied to North American soricid communities. J. Mammal. **73**: 491-503.

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 Theriol. **47**, Suppl. 1: 185-208.

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

Grant, P.R. 1972. Interspecific competition among rodents. V. Summary of the evidence for rodent species, and some generalisations. Annu. Rev. Ecol. Syst. **3**: 79-106.

Grant, P.R. 1976. Competition between species of small mammals (review). *In* Populations of small mammals under natural conditions. *Edited by* P.P. Snyder. University of Pittsburg, Pittsburg, Pymatuning Laboratory of Ecology, Special Publication No. **5**: 38-51.

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

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

Hanski, I. 1985. What does a shrew do in an energy crisis? *In* Behavioural ecology: Ecological consequences of adaptive behaviour. *Edited by* R.M. Sibly and R.H. Smith. Blackwell Scientific Publications, Oxford, the 25th Symposium of the British Ecological Society; pp. 247-252.

Hanski, I. 1994. Population biological consequences of body size in *Sorex*. *In* Advances in the biology of shrews. *Edited by* J.F. Merritt, G.L. Kirkland Jr., and R.K. Rose. Special Publication of Carnegie Museum of Natural History, Pittsburgh, No. **18**: 15-26.

Hanski, I., and Kaikusalo, A. 1989. Distribution and habitat selection of shrews in Finland. Ann. Zool. Fenn. **26**: 339-348.

Harper, S.J., and Batzli, G.O. 1997. Are staged dyadic encounters useful for studying aggressive behaviour of arvicoline rodents? Can. J. Zool. **75**: 1051-1058.

Hawes, M.L. 1977. Home range, territoriality and ecological separation in sympatric shrews *Sorex vagrans* and *Sorex obscurus*. J. Mammal. **58**: 354-367.

Johannesen, E., Brudevoll, J., Jenstad, M., Korslund, L., and Kristoffersen, S. 2002. Behavioural dominance of grey-sided voles over bank voles in dyadic encounters. Ann. Zool. 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. Zool. Zh. **77**: 838-849. [In Russian with English summary]

Kaufmann, J.H. 1983. On the definitions and functions of dominance and territoriality. Biol. Rev. Camb. Philos. Soc. **58**: 1-20.

Keddy, P.A. 1989. Competition. Chapman and Hall, London, New York.

Kirkland, G.L., Jr. 1991. Competition and coexistence in shrews (Insectivora: Soricidae). *In* The biology of the Soricidae. *Edited by* J.S. Findley and T.L. Yates. University of New Mexico, the Museum of Southwestern Biology, Albuquerque, Special Publication; pp. 15-22.

Krushinska, N.L., and Pucek, Z. 1989. Ethological study of sympatric species of European water shrews. Acta Theriol. **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*. J. Ethol. **11**: 11-21.

Krushinska, N.L., and Rychlik, L. 1994. Aggressiveness of a *Neomys fodiens* parous female towards conspecific and *N. anomalus* intruders. Acta Theriol. **39**: 329-332.

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

Kryštufek, B., Vohralík, V., and Kurtonur, C. 1998. A new look at the identity and distribution of water shrews (*Neomys* spp.) in Turkey. Z. Säugetierk. **63**: 129-136.

Kryštufek, B., and Vohralík, V. 2001. Mammals of Turkey and Cyprus: Introduction, checklist, Insectivora. Zgodovinsko društvo za južno Primorsko, Znanstveno-raziskovalno središče Republike Slovenije, Koper.

Langkilde, T., and Shine, R. 2004. Competing for crevices: interspecific conflict influences retreat-site selection in montane lizards. Oecologia, **140**: 684-691.

Law, R., Marrow, P., and Dieckman, U. 1997. On evolution under asymmetric competition. Evol. Ecol. **11**: 485-501.

Lehner, P.N. 1998. Handbook of ethological methods. 2nd edn. Cambridge University Press, Cambridge.

Lemen, C.A., and Freeman, P.W. 1983. Quantification of competition among coexisting heteromyids in the Southwest. Southwest. Nat. **28**: 41-46.

MacArthur, R.H. 1977. Geographical ecology: patterns in the distribution of species. Harper & Row, New York.

McNab, B.K. 1991. The energy expenditure of shrews. *In* The biology of the Soricidae. *Edited by* J.S. Findley and T.L. Yates. University of New Mexico, the Museum of Southwestern Biology, Albuquerque, Special Publication; pp. 35-45.

Martin, I.G. 1980. An ethogram of captive *Blarina brevicauda*. Am. Midl. Nat. **104**: 290-294.

May, R.M. 1981. Patterns in mult-species communities. *In* Theoretical ecology. Principles and applications. *Edited by* R.M. May. Blackwell Scientific Publications, Oxford, pp. 197-227.

Maynard Smith, J., and Parker, G.A. 1976. The logic of asymmetric contests. Anim. Behav. **24**: 159-175.

Michalak, I. 1982. Reproduction and behaviour of the Mediterranean water shrew under laboratory conditions. Säugetierk. Mitt. **30**: 307-310.

Miller Baker, A.E. 1974. Interspecific aggressive behaviour of pocket gophers *Thomomys bottae* and *T. talpoides* (Geomyidae: Rodentia). Ecology, **55**: 671-673.

Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Kryštufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J.B.M., Vohralik, V., and Zima, J. (*Editors*) 1999. The atlas of European mammals. T & AD Poyser Ltd., London.

Moraleva, N.V. 1989. Intraspecific interactions in the common shrew *Sorex araneus* in central Siberia. Ann. Zool. Fenn. **26**: 425-432.

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

Neet, C.R. 1989. Evaluation de la territorialité interspécifique entre *Sorex araneus* et *S. coronatus* dans une zone de syntopie (Insectivora, Soricidae). Mammalia **53**: 329-335.

Nevo, E., Naftali, G., and Guttman, R. 1975. Aggression patterns and speciation. Proc. Natl. Acad. Sci. U.S.A. **72**: 3250-3254.

Niethammer, J., and Krapp, F. (*Editors*) 1990. Handbuch der Säugetiere Europas. Band 3/I. Insektenfresser-Herrentiere. Aula-Verlag, Wiesbaden.

Oksanen, L., Fretwell, S.D., and Järvinen, O. 1979. Interspecific aggression and the limiting similarity of dose competitors: the problem of size gaps in some community arrays. Am. Nat. **114**: 117-129.

Oleinichenko, V.Yu. 2000. Behavior of the shrews *Sorex volnuchini* and *S. raddei*. Zool. Zh. **79**: 939-953. [In Russian with English summary]

Olsen, R.W. 1969. Agonistic behavior of the short-tailed shrew (*Blarina brevicauda*). J. Mammal. **50**: 494-500.

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

Persson, L. 1985. Asymmetrical competition: are larger animals competitively superior? Am. Nat. **126**: 261-266.

Pianka, E.R. 1981. Competition and niche theory. *In* Theoretical ecology. Principles and applications. *Edited by* R.M. May. Blackwell Scientific Publications, Oxford, pp. 167-196.

Platt, W.J. 1976. The social organisation and territoriality of short-tailed shrew (*Blarina brevicauda*) population in old field habitats. Anim. Behav. **24**: 305-318.

Putera, J.A., and Grant, W.E. 1985. Influence of behavioural interactions of spatial segregation of sympatric *Sigmoden*, *Baiomys*, *Reithrodentomys* populations. J. Mammal. **66**: 380-384.

Root, R.B. 1967. The niche exploitation pattern of the blue-grey gnatcatcher. Ecol. Monogr. **37**: 317-350.

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

Rychlik, L. 1998. Evolution of social systems in shrews. *In* Evolution of shrews. *Edited by* J.M. Wójcik and M. Wolsan. Mammal Research Institute, Białowieża, pp. 347-406.

Rychlik, L. 2000. Habitat preferences of four sympatric species of shrews. Acta Theriol. **45**, Suppl. 1: 173-190.

Rychlik, L. 2001. Habitat preferences of water shrews and root vole coexisting along a stream in Białowieża Forest. Säugetierk. Inf. **5**: 99-112.

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

Rychlik, L., and Jancewicz, E. 1998. Prey preferences and foraging behaviour in semi-aquatic and terrestrial shrews - cafeteria test. Abstracts of the Euro-American Mammal Congress, Santiago de Compostela, 19-24 July, 1998 (*Edited by* S. Reig). Santiago de Compostela, Spain: Universidade de Santiago de Compostela; p. 186.

Rychlik, L., and Jancewicz, E. 2002. Prey size, prey nutrition, and food handling by shrews of different body sizes. Behav. Ecol. **13**: 216-223.

Rychlik, L., and Ramalhinho, M.G. 2005. Habitat preferences of the Mediterranean water shrew *Neomys anomalus* in Portugal. *In* Advances in the biology of the Soricidae II. *Edited by* J.F. Merritt, S. Churchfield, R. Hutterer, and B.I. Sheftel. Special Publication 01 of the International Society of Shrew Biologists (ISSB), New York: 243-256.

Rychlik, L., Ruczyński, I., Borowski, Z., and Friedrich, T. 2004. Space use and competitive interactions in shrews (Insectivora: Soricidae) revealed by radio-telemetry. Contributions to the 5th International Symposium on Physiology, Behaviour and Conservation of Wildlife, Berlin, Germany, 26-29 September 2004 (*Edited by* C. Voigt and H. Hofer). Advances in Ethology 38, Suppl. to Ethology; p. 172.

Rychlik, L., and Zwolak, R. 2005. Behavioural mechanisms of conflicts avoidance among shrews. Acta Theriol. **50**: 289-308.

Schoener, T.W. 1983. Field experiments on interspecific competition. Am. Nat. **122**: 240-285.

Schröpfer, R. 1990. The structure of European small mammal communities. Zool. Jb. Syst. Ökol. Geogr. **117**: 355-367.

Shchipanov, N.A., Kalinin, A.A., Oleinichenko, V.Yu., and Demidova, T.B. 1998. General behavioural characteristics of shrews *Sorex araneus*, *S. caecutiens*, *S. minutus*, and *S. isodon* (Insectivora, Soricidae). Russ. J. Zool. **2**: 300-312.

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.

Taylor, J.R.E. 1998. Evolution of energetic strategies in shrews. *In* Evolution of shrews. *Edited by* J.M. Wójcik and M. Wolsan. Mammal Research Institute, Białowieża, pp. 309-346.

Tilman, D. 1987. The importance of the mechanisms of interspecific competition. Am. Nat. **129**: 769-774.

Wolff, J.O., and Dueser, R.D. 1986. Noncompetitive coexistence between *Peromyscus* species and *Clethrionomys gapperi*. Can. Field-Nat. **100**: 186-191.

Wolff, J.O., Freeberg, M.H., and Dueser. R.D. 1983. Interspecific territoriality in two sympatric species of *Peromyscus* (Rodentia: Cricetidae). Behav. Ecol. Sociobiol. **12**: 237-242.

Young, K.A. 2003. Evolution of fighting behavior under asymmetric competition: an experimental test with juvenile salmonids. Behav. Ecol. **14**: 127-134.

Zwolak, R. 2002. [Agonistic behaviour of shrews – a problem with postures]. Wiad. Ekol. **48**: 3-18. [In Polish with English abstract]

Zwolak, R., and Rychlik, L. 2004. Does the reduction of locomotor activity serve as an aggression avoidance mechanism in shrews (Soricidae)? Electr. J. Pol. Agricul. Univ., Biol. **7**(2) [online]. Available from http://www.ejpau.media.pl/series/volume7/issue2/biology/art-06.html.

Table 1. The number of tests (in brackets: *n* - number of obtained results)
in particular interspecific combinations

	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)

* - 11 results for *S. minutus* and 12 for *S. araneus.*

** - 9 results for *S. minutus* and 8 for *N. anomalus.*

FIGURE CAPTIONS

Fig. 1. Experimental design: conditions and duration of the four stages of tests.

Fig. 2. Percentage composition of different kinds of agonistic behaviours displayed by shrews during 5 minutes of the "open field" test-stage in interspecific interactions. Behaviours initiated reciprocally by each of the two opponents are illustrated by a separated bar; for example, in "*Sm-Sa*" combination the left bar represents duration of behaviours initiated by *Sorex minutus* towards *S. araneus*, whereas the right bar shows duration of behaviours initiated by *S. araneus* towards *S. minutus*. *n* = sample size (compare 'Methods' and Table 1).

Fig. 3. Mean (+SE) total duration of offensive behaviours displayed by shrews per 5 minutes during the three test-stages ("open-field", "food" and "shelter"). Values of $p \leq 0.05$ for differences between pairs of compared species (revealed by Mann-Whitney U-test) are shown over bars within the panels. Values of $p \leq 0.05$ for intraspecific differences between the consecutive test-stages (revealed by Wilcoxon test) are shown between the panels. Asterisks indicated significant differences after adjusting the levels of significance in both tests by False Discovery Rate procedure. See Fig. 2 for more explanations.

Fig. 4. Mean (+SE) total duration of defensive behaviours displayed by shrews per 5 minutes during the three test-stages. See Figs 2 and 3 for more explanations.

Fig. 5. Mean (+SE) total duration of threats displayed by shrews per 5 minutes during the three test-stages. See Figs 2 and 3 for more explanations.

Fig. 6. Mean (+SE) total time spent by shrews by food during the "food" test-stage. See Figs 2 and 3 for more explanations.

Fig. 7. (a) Mean (+SE) total time spent by shrews in the shelter during the "shelter" test-stage. (b) Final shelter residents, i.e. shrews remained in the shelter during the last minute of a test. Values of $p \leq 0.05$ for differences between pairs of compared species, revealed by Mann-Whitney U-test (a) and replicated goodness-of-fit test (b) are shown. Asterisks indicated significant differences after adjusting the levels of significance in both tests by False Discovery Rate procedure. See Fig. 2 for more explanations.

1. Separated (5 min)

partition

2. Open field (5 min)

3. Food (10 min)

4. Shelter (10 min)
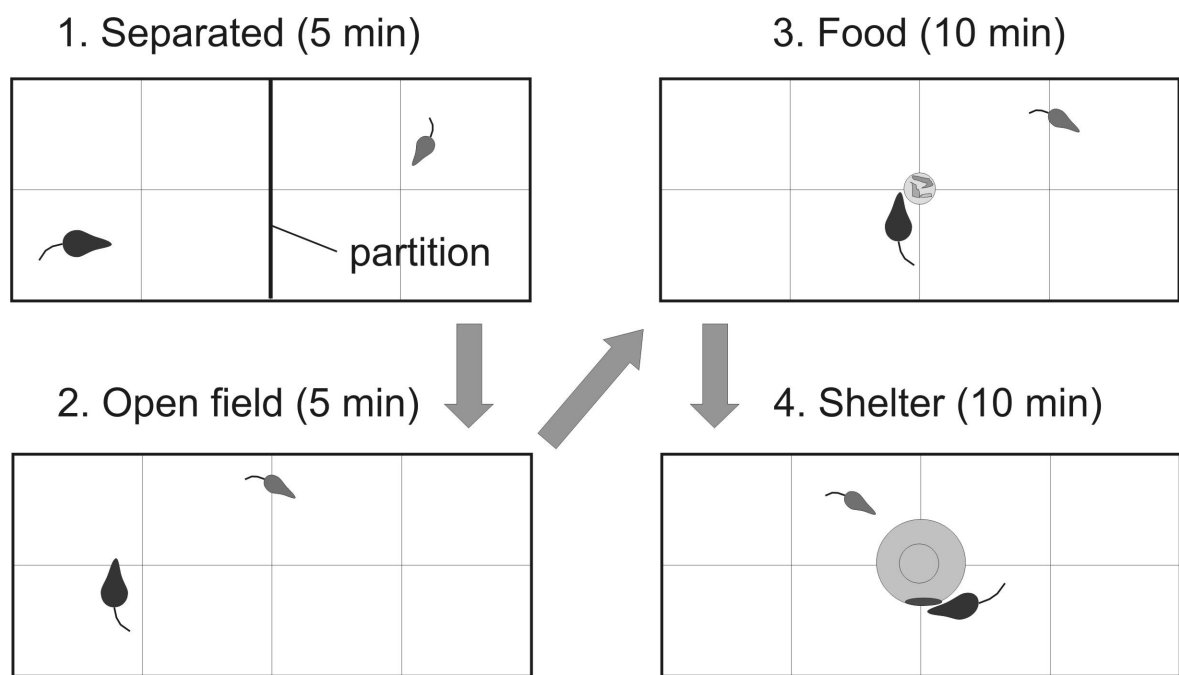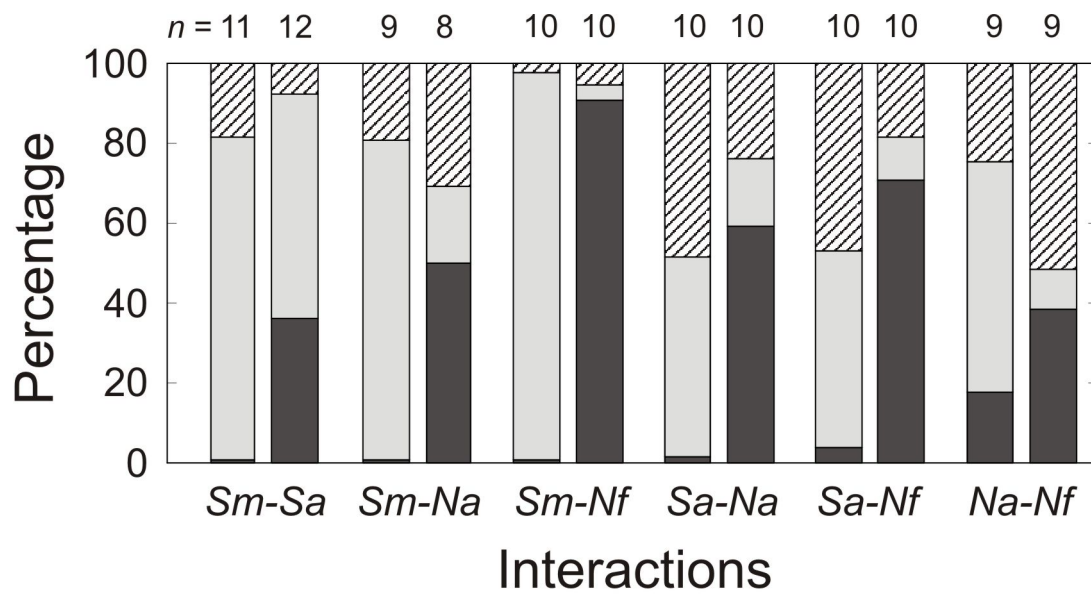
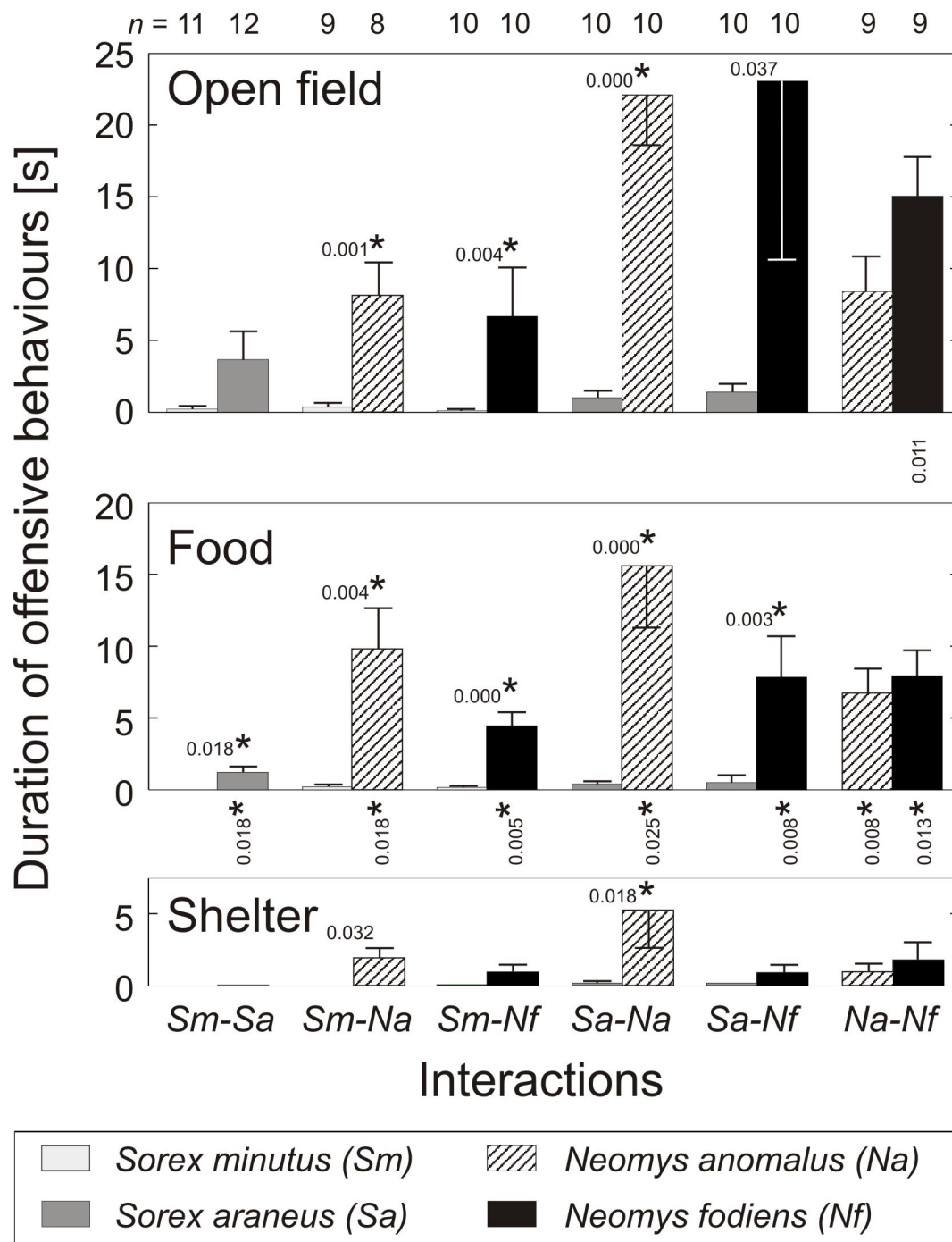Fig. 1. Rychlik and Zwolak

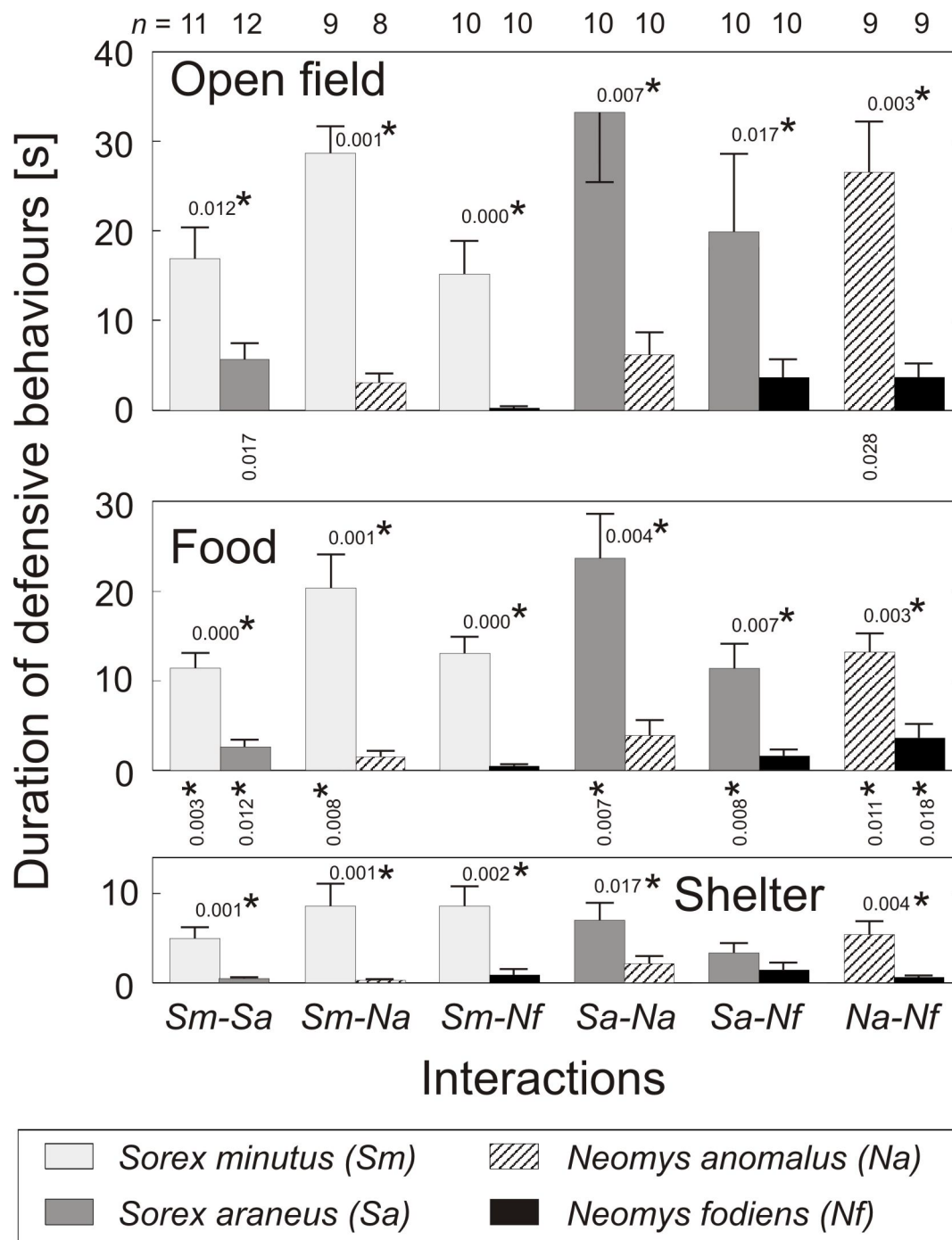Fig. 2. Rychlik and Zwolak

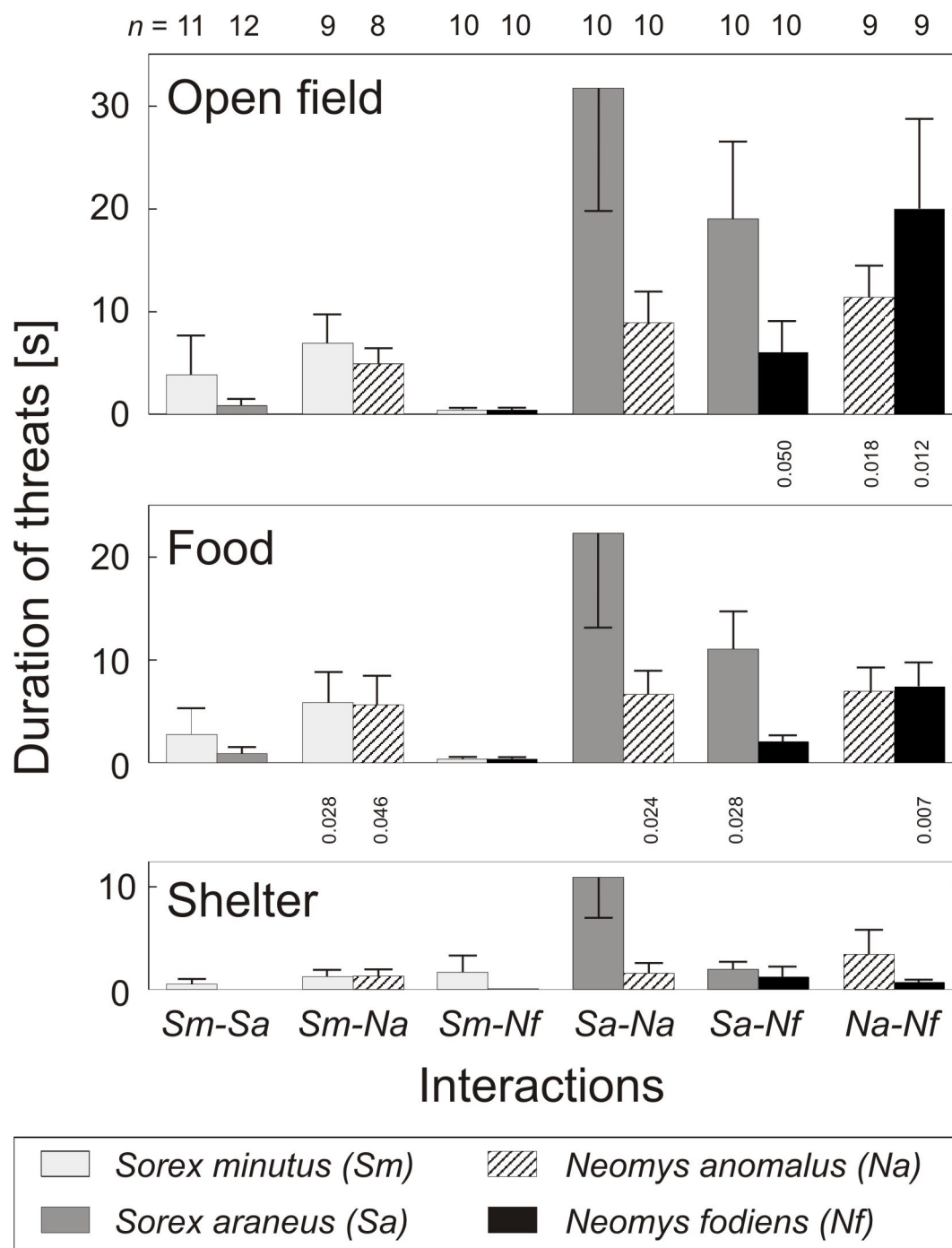Fig.3. Rychlik and Zwolak

Fig. 4. Rychlik and Zwolak
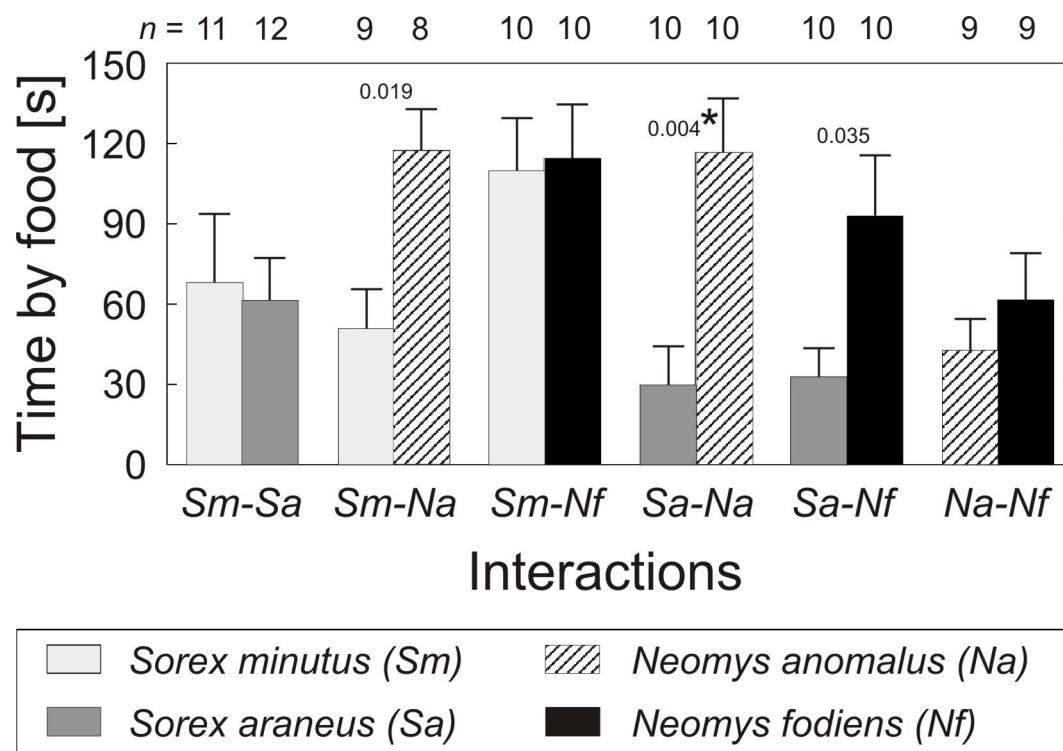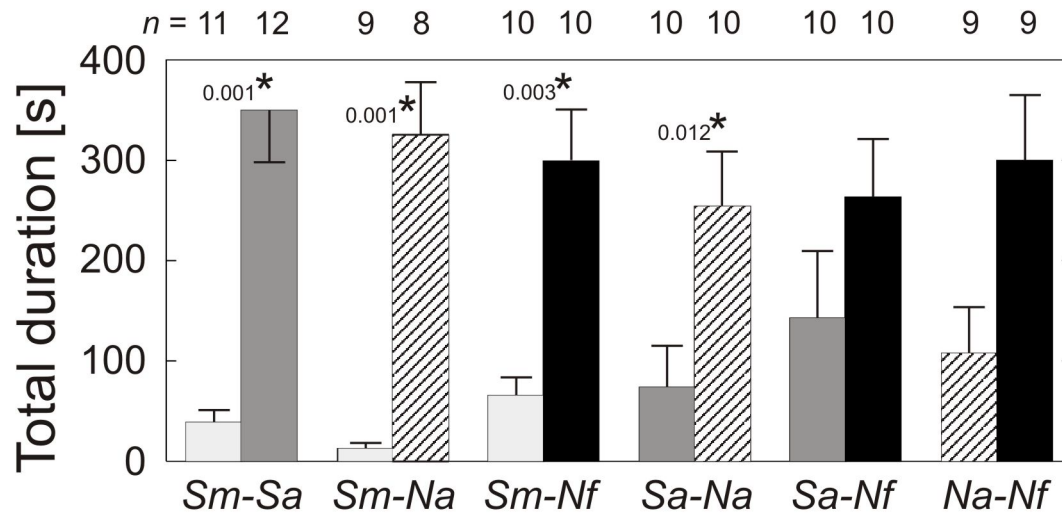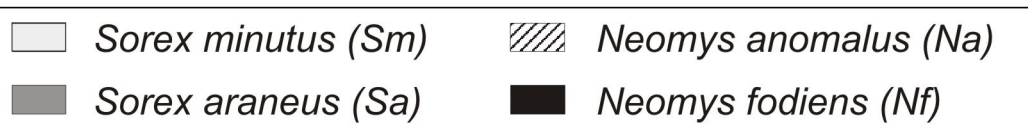
Fig. 5. Rychlik and Zwolak
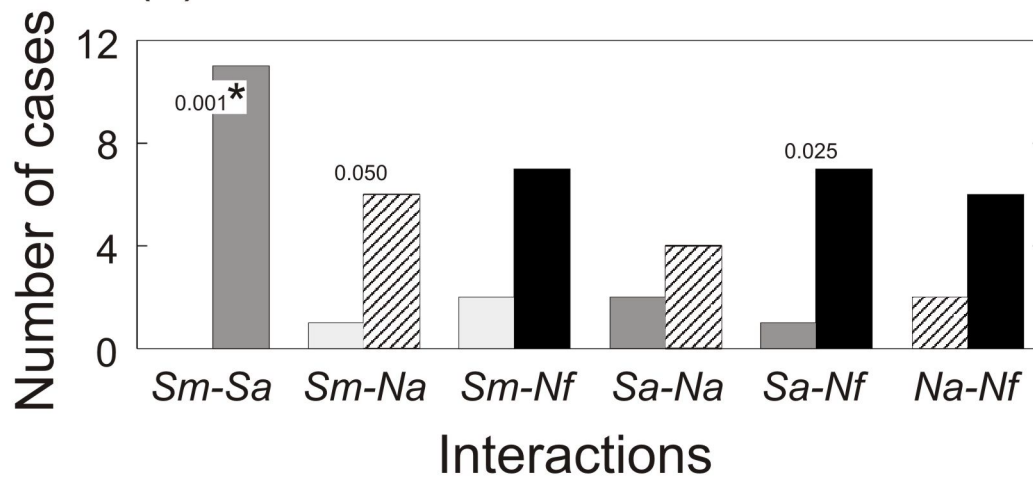
Fig. 6. Rychlik and Zwolak

(a) Time spent in the shelter

(b) Final shelter resident

Fig. 7. Rychlik and Zwolak