



## Social personality: a more social shrew species exhibits stronger differences in personality types



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Animal personalities have been studied extensively in the last decade. It is still not entirely understood, however, how different personalities evolve and persist. The social niche specialization hypothesis suggests that in group-living animals the combination of social conflicts and alternative options on how to deal with them are of key importance for the development and evolution of animal personality. Here we predicted that, following the social niche specialization hypothesis, a more social species should have more pronounced personality differences. We tested this prediction using four species of shrews that differ in ecology and sociability. Three species (*Neomys fodiens*, *Sorex araneus* and *Sorex minutus*) are strictly solitary outside the breeding season; the fourth species (*Neomys anomalus*) is intraspecifically more tolerant and able to live in groups. These four species offer a good model to assess our questions as *N. anomalus* can, in many other respects (e.g. body size, habitat, foraging mode), be considered as an ‘in-between’ species. We tested individuals of all species for their solitary activity and their activity and agonistic behaviour in within- and between-species dyadic encounters. We found that individuals of *N. anomalus*, but not the other species tested, showed consistent behavioural variation in agonistic behaviour. Consistent individual differences in activity were, however, also present in other species and activity was further correlated between the different contexts in all tested species. Finding more pronounced personality differences in *N. anomalus* than in the other, less sociable species supports the hypothesis that social niche specialization can influence the evolution of animal personalities.

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The interest in animal personality, i.e. consistent individual differences in behaviour across time and context, has been growing tremendously in the last decade. While a large amount of theoretical and empirical work has already been conducted (e.g. Bell, Hankison, & Laskowski, 2009; Dall, Bell, Bolnick, & Ratnieks, 2012; Sih, Bell, Johnson, & Ziemba, 2004; Wolf & Weissing, 2012), it is still not entirely understood how different personalities evolve and persist. Several theoretical approaches have been taken to try to explain the existence of between-individual differences from an adaptive perspective (Biro & Stamps, 2008; Dall, Houston, & McNamara, 2004; Dingemanse & Wolf, 2010; Wolf & Weissing, 2010).

One promising concept is that of state – behaviour feedback loops (reviewed in Sih et al., 2015). The state of an animal includes all its individual features (e.g. its hormone levels or age) and external characteristics (e.g. the population density or sex ratio)

that affect the costs and benefits of its behavioural actions. If the behaviour of the animal in turn affects its state, resulting in a feedback loop between state and behaviour, consistent individual differences can arise (Sih et al., 2015).

An important aspect of an individual's state is its social status. Positive feedback loops can emerge if different social roles cause differences in behaviour that in turn reinforce the respective social roles of the interacting individuals, resulting in a reinforcement of the so-called social niches.

The concept of social niches can be understood analogously to that of the ecological niche. While the ecological niche of an animal comprises the conditions and resources it needs to practise its way of life (Begon, Townsend, & Harper, 2005), its social niche encompasses the social conditions it needs to do so. These social conditions are shaped by interactions with conspecifics, leading to situations where different individuals can and typically do choose between different social roles.

The social niche specialization hypothesis suggests that in group-living animals the combination of social conflicts and alternative options on how to deal with them are of key importance for the development and evolution of animal personality (Bergmüller

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& Taborsky, 2010; Montiglio, Ferrari, & Réale, 2013). Repeated social conflicts among individuals of one group can be solved either on a case by case basis, each time competing for and then switching to a specific role, or by adopting consistent individual differences. The latter is assumed to be less costly and should thus be favoured (Bergmüller & Taborsky, 2010; DeWitt, Sih, & Wilson, 1998).

Differences in personality between individuals can thus be understood as social niche specialization (Bergmüller & Taborsky, 2010; Montiglio et al., 2013; Sih et al., 2015) and we can use the concept of social niches to try to explain the evolution and maintenance of consistent individual differences in behaviour (reviewed in Bergmüller & Taborsky, 2010). An example of a positive feedback loop between social status and behaviour is that of foraging patch choice: when subordinate individuals forage in low-quality patches to avoid competition, this patch choice can in turn prevent them from obtaining the resources required to gain dominance, thereby reinforcing their subordinate position (Rands, Pettifor, Rowcliffe, & Cowlshaw, 2006).

It seems obvious that feedback loops between social state and behaviour should have more leverage in a species that shows more social behaviour, as it faces a larger number and variety of different social situations than a less social species. In such a species, the repeated social interactions with other individuals can drive personality differences. We hypothesized that consequently a more social species should have more pronounced personality differences, i.e. we expect a higher between-individual variation in personality types in social than not social species. Surprisingly, this simple prediction has, to the best of our knowledge, only been tested once: in a genus of spiders with a large variation in social structure between species, those species that are more social did indeed exhibit a larger within-species variation in behavioural types (Pruitt, Oufiero, Avilés, & Riechert, 2012).

In this study we tested this hypothesis for the first time in vertebrates (mammals) using four species of shrews that differ in ecology and sociability. While three species (*Neomys fodiens*, *Sorex araneus* and *Sorex minutus*) are strictly solitary across all seasons (with the exception of a few hours each year dedicated to mating), the fourth species (*Neomys anomalus*) has a higher overlap of home ranges than *N. fodiens* or *S. araneus* (Rychlik, Ruczynski, Borowski, & Friedrich, 2004), is intraspecifically tolerant and is able to live in groups, at least outside the reproductive season (Rychlik, 1998). These four species offer a good model to assess our questions as *N. anomalus* can, in many other respects, be considered as an 'in-between' species: its body size lies between that of the larger *N. fodiens* and the smaller *Sorex* species, its typical habitat lies closer to bodies of water than that of the *Sorex* species, but its foraging mode is not so tightly connected with water as that of *N. fodiens* (Churchfield & Rychlik, 2006; Rychlik, 2000; Table 1). Nevertheless, our previous studies suggest that the more social *N. anomalus* has a wider repertoire of behavioural options than the strictly solitary shrews. For example, the number of conflicts among *N. anomalus* in a newly established social group was significantly higher than in

the solitarily living *N. fodiens*. However, the conflict frequency among *N. anomalus* quickly decreased over time, whereas it remained at the same level in *N. fodiens* (Krushinska & Rychlik, 1993; Krushinska, Rychlik, & Pucek, 1994). Such a distinct and repeated reduction of conflicts among *N. anomalus* could result, for example, from different social roles established among group members. Moreover, *N. fodiens* displayed almost exclusively antagonistic interactions, whereas more than half of the total number of interactions among *N. anomalus* were neutral-investigative (Krushinska & Rychlik, 1993).

We tested the link between sociability and personality differences using two types of behaviour that are ecologically relevant personality measures (Sih, Bell, & Johnson, 2004): activity and agonistic behaviour. Both behaviours are important for the studied shrew species, as they coexist with highly overlapping ecological niches (Churchfield & Rychlik, 2006; Rychlik, 2000, 2005). Therefore, their activity and the agonistic interactions (within and between species, as elements of interference competition) are crucial for securing resources and thus for their fitness (Dickman, 1991; Rychlik & Zwolak, 2006). If the proposed concept of the evolution of animal personalities is true, we expect *N. anomalus* to have more pronounced personality differences than the other, less sociable species.

## METHODS

### Animals and Housing

Wild shrews were live-trapped with pitfalls in Białowieża Forest (eastern Poland) during the summers of 2000–2002. Pitfalls contained some moss for bedding, minced beef as bait/food and were covered with a roof to protect them from rain. Traps were opened in the afternoon (ca. 1700) and checked every 2–2.5 h until the early night hours (ca. 2400). Trapping was not performed during heavy rainfall or cold evenings. Only subadult individuals (i.e. young of the year, fully grown but sexually immature) were used in the experiments, while all adult shrews were released instantly upon capture. Adults are reproductively active during summer, so they were easily distinguished by nipples and/or signs of pregnancy visible in females or enlarged testes in males. In addition, adults are generally larger than subadults. Animals were transported in buckets containing some cotton bedding and food. Transport lasted 10–20 min. In the laboratory, shrews were placed in individual cages (30 × 40 cm and 15 cm high), where they were acclimatized to conditions of captivity for at least 5 days. The cages were equipped with a shelter (an upside down 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%. Most shrews were kept

**Table 1**  
Size, ecology and sociability of the tested shrew species

Species	Body mass (g) <sup>1</sup>	Habitat <sup>2</sup>	Foraging mode <sup>3</sup>	Sociability <sup>4</sup>
<i>Neomys fodiens</i>	14.4	Adjacent to water	Aquatic (diving and wading) and terrestrial (epigeal and hypogeal)	Solitary
<i>Neomys anomalus</i>	9.8	Close to water	Aquatic (mainly wading) and terrestrial (epigeal and hypogeal)	Gregarious
<i>Sorex araneus</i>	7.4	Rather wet, usually several metres away from water	Only terrestrial (mainly hypogeal, also epigeal)	Solitary
<i>Sorex minutus</i>	2.8	Rather wet, often close to water	Only terrestrial (mainly epigeal, also scansorial)	Solitary

<sup>1</sup> Mean body masses of animals tested in this study.

<sup>2</sup> Rychlik (2000).

<sup>3</sup> Churchfield and Rychlik (2006); Rychlik (1997).

<sup>4</sup> Krushinska and Rychlik (1993, 1998).

for approximately 3 weeks and none was kept for longer than 8 weeks. After testing, shrews were released at the site of capture.

We tested a total of 70 subadult individuals: 17 pygmy shrews, *S. minutus*, 19 common shrews, *S. araneus*, 16 Mediterranean water shrews, *N. anomalus*, and 18 Eurasian water shrews, *N. fodiens*. We cannot exclude the possibility that some of these shrews were siblings, but as animals were captured in several different sites and over a few successive years, such instances were probably rare. It was impossible to determine the sex of the tested individuals, but the social behaviour of subadult males and females is similar (Rychlik, 1998).

#### Test Procedure

To test our predictions, we performed dyadic encounters in a neutral arena, a method frequently used to investigate inter- and intraspecific interactions in small mammals such as shrews (e.g. Baxter & Irwin, 1995; Harper & Batzli, 1997; Kalinin, Shchipanov, & Demidova, 1998; Pasch, Bolker, & Phelps, 2013).

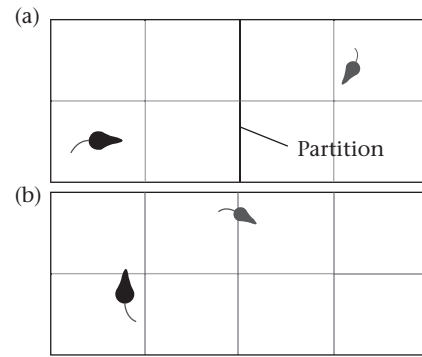
Animals were tested in a separate room during daytime, i.e. during a period of lower activity of shrews (their activity peaks between 2000 and 0100, but shrews are active around the clock: Rychlik, 2005). The set-up (neutral arena) consisted of a bare glass terrarium measuring 70 × 30 cm and 40 cm high. The arena was illuminated with white light and filmed from above (Sony SSC-C370P camera, Panasonic NV-FS100HQ video recorder, Sony KV-X2531B monitor). To score activity, the area of the terrarium was divided into eight rectangles (each 30 × 33 cm), four on each side (Fig. 1), by placing a sheet of paper with line markings below its floor.

Each trial lasted 10 min and consisted of two consecutive parts. For the first part (habituation phase, 5 min) the terrarium was divided in half by a semitransparent plastic partition. Two shrews were placed separately into each side of the neutral arena. During experiments, both individuals were treated equally, but for statistical analysis, each individual in a given trial was treated once as a focal and once as a stimulus animal. During this stage, the shrews could habituate and explore their new surroundings without physical contact with the other individual. We did not observe any reactions to the stimulus individual in this stage of the test (see also Results: Influence of trial and stimulus species on behaviour and Table 5 in the Results). For the second part (encounter phase, 5 min), the partition was removed and the animals could interact. After a trial was completed, both shrews were placed back into their home terraria, and the set-up was carefully washed with water and detergent.

Each individual took part in one to four trials (mean 2.3), with differing species as stimulus individuals. Consecutive trials of the same individual were separated by at least a 3-day break. A total of 87 encounter trials were conducted, with each encounter analysed twice: once for each of the two individuals considered as the focal individual, the other as the stimulus individual. This resulted in 174 individual behavioural trials being analysed. The number of trials per species combination is presented in Table 2. This design of repeated trials for each individual with different stimulus species allowed us to test the effect of trial number and stimulus species on the behavioural parameters measured.

#### Ethical Note

Capturing of shrews was conducted under 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 of Poland. Trapping, housing and experimental procedures were conducted under approval (no. 2001/11 of 11 January



**Figure 1.** Experimental set-up in (a) habituation and (b) encounter phase. The set-up is a glass terrarium measuring 70 × 30 cm and 40 cm high.

**Table 2**

Number of encounters between all possible combinations of the tested shrew species

Focal species	Stimulus species			
	<i>Nf</i>	<i>Na</i>	<i>Sa</i>	<i>Sm</i>
<i>Nf</i>	6	11	9	10
<i>Na</i>	–	7	12	11
<i>Sa</i>	–	–	6	12
<i>Sm</i>	–	–	–	3
Total number of encounters				87
Total number of individual encounters <sup>1</sup>				174

*Nf* = *Neomys fodiens*, *Na* = *Neomys anomalus*, *Sa* = *Sorex araneus*, *Sm* = *Sorex minutus*.

<sup>1</sup> Each encounter was analysed twice, once for each of the two involved individuals.

2001) from the Local Ethical Commission for Experiments with Animals in Białystok (Poland). The animals were also cared for in accordance with the ASAB/ABS Guidelines for the treatment of animals in behavioural research and teaching (ASAB/ABS, 2012). We planned to stop all conflicts that posed a threat to the health of the animals (i.e. if we observed any signs of bleeding, combat lasting over 15 s or harassment of a submissive shrew by a dominant lasting over 30 s). However, we did not have to interrupt any tests. None of the animals died during or following a trial. We tried to reduce disturbance or distress in the tested shrews by avoiding any handling of them between tests. Hence, during the time spent in captivity, shrews did not display any visible signs of distress, they behaved normally and the majority of them increased their body mass (average increase 1.8%).

#### Quantifying Behaviour

We quantified two types of behaviour: activity and agonistic behaviour. Activity was scored in both habituation and encounter phases, agonistic behaviour self-evidently only in the encounter phase. Activity was measured as the total count of lines crossed during each of the phases. From the recorded videos, we extracted numerous categories of agonistic and neutral behaviour (for details see Rychlik & Zwolak, 2005, 2006). As we here aimed to test differences in aggressive behaviour, we used only those categories in our analysis that were either clearly offensive or clearly defensive, i.e. those agonistic behaviours in which a shrew was either moving towards the other individual (different chasing or attacking behaviours = offensive) or moving away from the other individual (different escaping behaviours = defensive, Table 3). We checked the validity of placing the measured behavioural categories into the

**Table 3**  
Types of scored behaviours

Group	Abbreviation	Description
Defensive	DEF	Backing off from other individual
		Escaping from other individual
Offensive	OFF	Following other individual (slow, at some distance)
		Chasing other individual (quick, at a short distance)
		Attacking other individual (with or without contact)
		Fighting with other individual

two behavioural groups (offensive or defensive) by calculating Spearman correlation coefficients between these categories with Bonferroni correction for multiple testing. Behavioural categories were all positively correlated within the behavioural groups (14 of 22 correlations within groups were significant after correction; the results of these correlations can be found in the [Supplementary Material](#)). Correlations between the two behavioural groups (offensive and defensive) were weak, mostly negative and nonsignificant. Offensive and defensive behaviour were both measured as number of occurrences and duration of a specific type of behaviour during the encounter phase. As we found strong positive correlations between number and duration of each defensive and offensive behaviour (Spearman correlation coefficient: defensive behaviour:  $r = 0.98$ ,  $P < 0.05$ ; offensive behaviour:  $r = 1.00$ ,  $P < 0.05$ ), we only used the number of behavioural events for further analysis. The resulting behavioural parameters were activity in the habituation phase and the encounter phase (HAB and ENC, in line crossings per phase) and offensive and defensive behaviour in the encounter phase (OFF and DEF, in number of behavioural bouts).

#### Statistical Analysis

All statistical tests were carried out using R ([R Core Team, 2014](#)).

#### Correlation between behavioural parameters

Correlations between different types of behaviour can indicate behavioural syndromes ([Sih, Bell, & Johnson et al., 2004](#)). We thus tested for correlation between the four behavioural parameters (HAB, ENC, OFF and DEF) by calculating Spearman correlation coefficients using individual means.  $P$  values were corrected for multiple testing using Bonferroni correction ( $=P'$ ).

We further tested the within-individual correlation for each behavioural parameter using Spearman correlation coefficients, conducted for all individuals that participated in at least two trials (for those individuals that had participated in more than two trials, only the first two were used for correlations).

#### Repeatability within species and influence of predictors

To calculate individual repeatability, we ran generalized linear mixed models with Markov chain Monte Carlo (MCMC) estimation. MCMC is a Bayesian statistical method that can be used for fitting non-Gaussian distributions and is often used for the analysis of animal personalities ([Dingemans & Dochtermann, 2013](#)). We ran 12 separate models, for each of the four species on each of the three response variables (HAB, ENC, OFF). We applied the function `MCMCglmm` from the R package `MCMCglmm` ([Hadfield, 2010, 2015](#)), using noninformative proper priors for Poisson variance distribution. We ensured convergence and adequate chain mixing by checking the posterior distributions and autocorrelations (less than 0.1) between successively stored iterations of five independent chains per model, all run with 500 000 iterations, a 1000 burn-

in period and thinning every 500 iterations for each model ([Hadfield, 2010](#)). From the results of the models, we calculated the repeatability values for each species and each response variable.

From the resulting models, we further obtained the effect of the two predictors (trial number and stimulus species) on the behavioural parameters.

## RESULTS

### Correlations between Behavioural Parameters and within Individuals

In all species, we found positive correlations between the activity in the habituation and in the encounter phase. These were highly significant in *N. anomalus* and *S. minutus* (*N. anomalus*:  $r = 0.76$ ; *S. minutus*:  $r = 0.87$ ; both  $P' < 0.01$ ), significant in *N. fodiens* ( $r = 0.64$ ,  $P' = 0.02$ ) and nonsignificant in *S. araneus* ( $r = 0.53$ ,  $P' = 0.12$  with Bonferroni correction,  $P < 0.05$  without).

Within-individual correlation was high for activity in both habituation and encounter phases and for offensive behaviour, but not for defensive behaviour (HAB:  $r = 0.64$ ; ENC:  $r = 0.59$ ; OFF:  $r = 0.60$ ; all  $P' < 0.05$ ; DEF:  $r = 0.08$ ,  $P' = 0.56$ ). We thus did not include defensive behaviour in our further analysis of individual differences (but we kept it for analyses of species differences).

### Behavioural Variability at the Species Level

The tested species displayed different amounts of variance in their behaviour. The within-species variances of activity differed between species in the habituation phase (Levene's test:  $F_3 = 10.283$ ,  $P < 0.001$ ), but not in the encounter phase ( $F_3 = 0.762$ ,  $P = 0.517$ ). The variances of defensive ( $F_3 = 2.986$ ,  $P = 0.033$ ) and offensive behaviour ( $F_3 = 10.557$ ,  $P < 0.001$ ) also differed between species. The variance of activity in the habituation phase was higher in *N. anomalus* than in the other three species; the variance of offensive behaviour was higher in both *Neomys* species than both *Sorex* species ([Fig. 2](#)).

### Individual Repeatability within Species

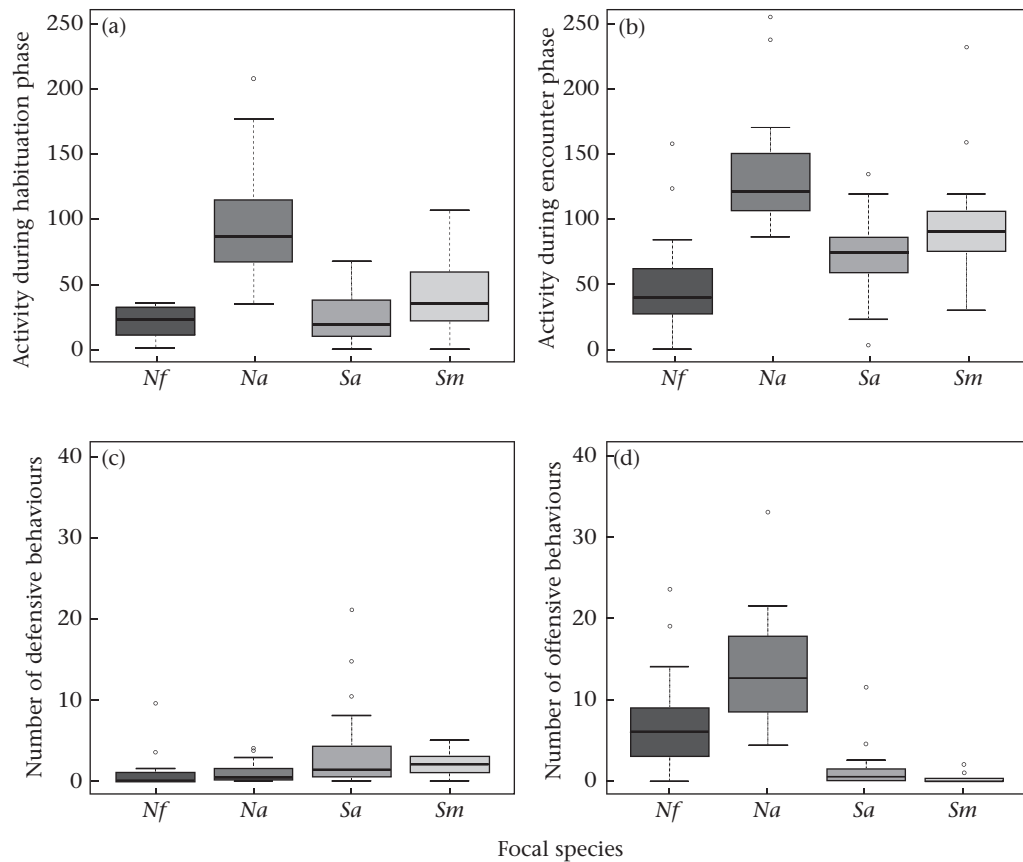
To test for personalities, we calculated repeatability values using generalized linear mixed models with Markov chain Monte Carlo (MCMC) estimation. Repeatability was high (over 0.4) for activity in three of four species ([Table 4](#)). Activity was highly repeatable for *N. anomalus* and *S. araneus* during the habituation and encounter phases, but for *S. minutus* only during the encounter phase. *Neomys anomalus* was the only species with a high repeatability in offensive behaviour.

### Influence of Trial and Stimulus Species on Behaviour

*Neomys anomalus* significantly increased activity with an increasing number of trials in both the habituation phase and the encounter phase ([Fig. 3, Table 5](#)). *Sorex araneus* showed a slightly lower activity during encounter trials when meeting members of their own species.

Stimulus species had a significant influence on the level of offence in both *Neomys* species. *Neomys fodiens* showed more offensive behaviour when meeting *N. anomalus* (median 11 s) or members of their own species (7 s) than when encountering either of the two *Sorex* (*S. araneus* 3 s, *S. minutus* 3 s) species. *Neomys anomalus* displayed lower levels of offensive behaviour when encountering *N. fodiens* (7 s) or *S. minutus* (7 s), and higher levels when encountering members of their own species (17 s) or individuals of the similar sized *S. araneus* (19 s).





**Figure 2.** Behavioural differences between the four tested shrew species. (a) Activity during habituation phase, (b) activity during encounter phase, (c) number of defensive behaviours, and (d) number of offensive behaviours. Boxes denote the first, second and third quartiles and whiskers the 1.5 interquartile range; dots are outliers. See Table 2 for species abbreviations.

**Table 4**  
Repeatability values of the four shrew species for each of the three behavioural parameters

Parameter	Species			
	<i>N. fodiens</i>	<i>N. anomalus</i>	<i>S. araneus</i>	<i>S. minutus</i>
HAB	0.005 (0.0002–0.6115)	<b>0.757</b> (0.3861–0.8752)	<b>0.409</b> (0.0005–0.7492)	0.008 (0.0003–0.8676)
ENC	0.003 (0.0002–0.4312)	<b>0.503</b> (0.0228–0.6867)	<b>0.695</b> (0.2862–0.8331)	<b>0.857</b> (0.2862–0.9539)
OFF	0.005 (0.0002–0.571)	<b>0.451</b> (0.0218–0.5892)	0.004 (0.0000–0.8426)	0.005 (0.0001–0.9941)

The estimates were obtained from MCMCglm models and are presented with the 95%-confidence intervals. Cases with high repeatability (those where  $r > 0.45$ , as opposed to all others, where  $r < 0.01$ ) are printed in bold. HAB = activity in habituation phase, ENC = activity in encounter phase, OFF = level of offensive behaviour.

Activity and offensive behaviour in *S. minutus* were unaffected by the analysed factors (Table 5). We found no influence of partner species on the behaviour of animals during the habituation trials, where the two parts of the test terrarium were separated by a plastic partition (Table 5).

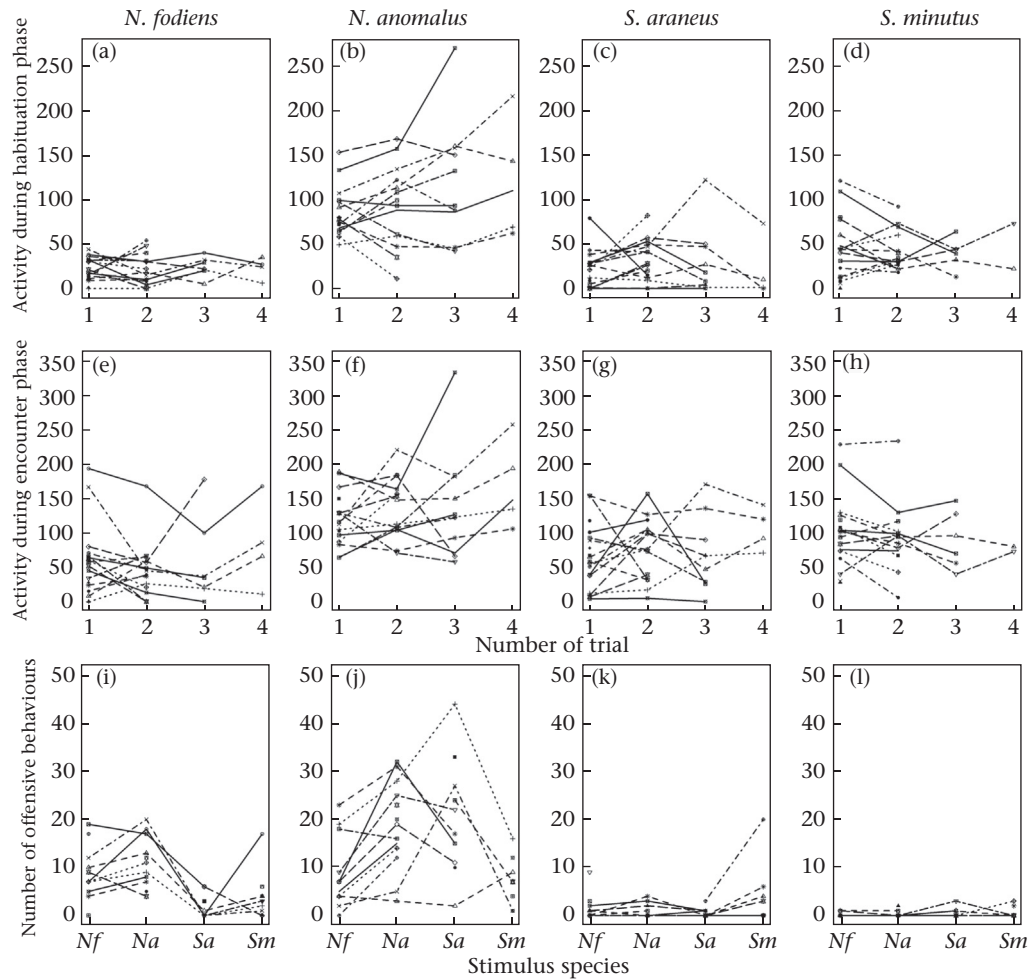
## DISCUSSION

### *Neomys anomalus* Shows Consistent Individual Differences in Social Behaviour

Following the social niche specialization hypothesis, we had predicted that the more social *N. anomalus* should have more pronounced personality differences than the three less sociable species. Indeed, we found that individuals of *N. anomalus*, but not the other species tested, showed high individual repeatability in agonistic behaviour in between- and within-species dyadic

encounters: some individuals of *N. anomalus* were less offensive than others and these differences persisted across trials.

Different personality types in social animals might ease group living, with some individuals behaving rather dominantly and others rather submissively. Sociability and social niches are an important part of social dynamics and have been shown to relate to personality differences in a wide range of animal taxa (reviewed in Bergmüller & Taborsky, 2010). Examples include territory maintenance in cooperatively breeding cichlid fish, *Neolamprologus pulcher* (Bergmüller & Taborsky, 2007) and the repeatability of boldness-like behaviour in the social spiders *Stegodyphus mimosarum* and *Stegodyphus dumicola* (Laskowski & Pruitt, 2014; Modlmeier et al., 2014). In female meerkats, *Suricata suricatta*, a more complex relation between social behaviour and social role has been found, where individuals seem to switch social roles at dominance acquisition (Carter, English, & Clutton-Brock, 2014). However, social niche specialization might not always be able to



**Figure 3.** Individual behavioural differences in the four tested shrew species. (a–d) Activity during habituation phase against trial number. (e–h) Activity during encounter phase against trial number. (i–l) Number of offensive behaviours against stimulus species. Each line represents one individual. Line patterns and symbols are randomly chosen for better readability. See Table 2 for species abbreviations.

explain differences in personality types. For example, in three-spined sticklebacks, *Gasterosteus aculeatus*, repeated social interactions did not increase the between-individual variation in a social foraging task; rather, the social foraging behaviour of individuals was related to their behavioural type (Laskowski & Bell, 2014). As the two possible explanations for between-individual variation compared in this study (social interactions and behavioural type of the individual) are nonexclusive, it might be possible, however, that the experiment failed to capture the full effects of repeated social interactions on the behaviour of the sticklebacks.

Social interactions are likely to explain between-individual variation in some, but not all species or cases (Magnhagen & Bunnefeld, 2009; Staffan, Magnhagen, & Alanärä, 2002). Animal personality research generally focuses on the comparison of individuals within one species, including studies on the relation between social behaviour and personality. The results of these studies are diverse and depend on the studied species and ecological context. For example, more social individuals of a given species have been shown to be less anxious (*Microtus arvalis*, Lantová, Šichová, Sedláček, & Lanta, 2011) or more aggressive (*Rhabdomys pumilio*, Schoepf & Schradin, 2012) on the one hand, but less bold (*G. aculeatus*, Laskowski & Bell, 2014), less explorative (*Estrilda astrild*, Carvalho et al., 2013) or less active (*Taeniopygia guttata*, McCowan & Griffith, 2015), on the other. The context dependence

of the relation between social and other behaviours in one species has been convincingly demonstrated in great tits, *Parus major*, where the pace of exploration had a positive influence on dominance status in territorial mature males, but a negative one in nonterritorial young males (Dingemanse & de Goede, 2004).

Only a few studies have investigated personalities in closely related species that differed in social organization or social behaviour (Fragaszy & Mason, 1978; Kiesel, Sneker, Ruhl, & McRobert, 2012). These studies showed a relation between social behaviour and other personality traits. However, they did not compare the degree of personality differences between the species. Our study fills this gap (see also Pruitt et al., 2012). We found that the more sociable *N. anomalus* exhibited stronger personality differences than the three nonsociable shrew species we tested: this result supports the social niche hypothesis. Our results are also consistent with the findings of Pruitt et al. (2012), who used a similar, comparative interspecies approach and demonstrated that sociality in spiders was positively correlated with an increased within-species variation in aggressiveness and boldness.

The social niche specialization hypothesis (Bergmüller & Taborsky, 2010) suggests that consistent individual differences in behaviour can arise when a species or population faces strong intraspecific competition for limited resources such as food, space or breeding opportunities. This, in turn, could be additionally

**Table 5**

The influence of trial number (Trial) and stimulus species (Stim.Sp.) on activity and offensive behaviour during dyadic encounters of shrews in a neutral arena

Species		Posterior mean	Lower 95% CI	Upper 95% CI	PMCMC
<i>Neomys fodiens</i>					
HAB	(Intercept)	<b>2.4311</b>	<b>1.4010</b>	<b>3.4852</b>	<b>&lt;0.001</b>
	Trial	0.1272	-0.2252	0.4354	0.4670
	Stim.Sp.Nf	0.3096	-0.4477	1.1059	0.4030
	Stim.Sp.Sa	-0.1592	-1.1129	0.8102	0.7490
	Stim.Sp.Sm	0.0910	-0.7930	0.9493	0.8160
ENC	(Intercept)	<b>2.8924</b>	<b>1.2866</b>	<b>4.3975</b>	<b>0.0040</b>
	Trial	0.1763	-0.3541	0.6695	0.4870
	Stim.Sp.Nf	-0.1324	-1.2948	1.0543	0.7976
	Stim.Sp.Sa	0.0986	-1.4772	1.4691	0.8998
	Stim.Sp.Sm	0.5384	-0.7489	1.8291	0.4008
OFF	(Intercept)	<b>2.0547</b>	<b>1.1674</b>	<b>2.9212</b>	<b>&lt;0.001</b>
	Trial	0.0912	-0.2059	0.3816	0.5231
	Stim.Sp.Nf	-0.3849	-1.0194	0.2947	0.2605
	Stim.Sp.Sa	<b>-1.5586</b>	<b>-2.4473</b>	<b>-0.6888</b>	<b>0.0020</b>
	Stim.Sp.Sm	<b>-1.1778</b>	<b>-1.9300</b>	<b>-0.3524</b>	<b>0.0060</b>
<i>Neomys anomalus</i>					
HAB	(Intercept)	<b>3.9651</b>	<b>3.4850</b>	<b>4.4251</b>	<b>&lt;0.001</b>
	Trial	<b>0.1626</b>	<b>0.0509</b>	<b>0.2896</b>	<b>0.0080</b>
	Stim.Sp.Nf	0.2665	-0.0788	0.5361	0.0782
	Stim.Sp.Sa	0.2253	-0.1129	0.6201	0.2084
	Stim.Sp.Sm	0.1404	-0.1710	0.4279	0.3487
ENC	(Intercept)	<b>4.4129</b>	<b>4.0194</b>	<b>4.7884</b>	<b>&lt;0.001</b>
	Trial	<b>0.1463</b>	<b>0.0481</b>	<b>0.2571</b>	<b>0.0060</b>
	Stim.Sp.Nf	0.0149	-0.2719	0.2967	0.9078
	Stim.Sp.Sa	0.2896	-0.0283	0.6349	0.0922
	Stim.Sp.Sm	0.1614	-0.1313	0.4673	0.3126
OFF	(Intercept)	<b>2.7242</b>	<b>1.9379</b>	<b>3.4437</b>	<b>&lt;0.001</b>
	Trial	0.0079	-0.1902	0.2201	0.9460
	Stim.Sp.Nf	<b>-0.7504</b>	<b>-1.2693</b>	<b>-0.1595</b>	<b>0.0100</b>
	Stim.Sp.Sa	-0.0707	-0.6628	0.5620	0.8160
	Stim.Sp.Sm	<b>-1.1145</b>	<b>-1.6786</b>	<b>-0.4877</b>	<b>&lt;0.001</b>
<i>Sorex araneus</i>					
HAB	(Intercept)	<b>2.4577</b>	<b>1.2109</b>	<b>3.7544</b>	<b>&lt;0.001</b>
	Trial	-0.0280	-0.5989	0.4624	0.8800
	Stim.Sp.Nf	0.0156	-1.1324	1.1580	0.9960
	Stim.Sp.Sa	-0.2473	-1.5916	1.0657	0.6710
	Stim.Sp.Sm	0.3016	-0.7790	1.5222	0.5750
ENC	(Intercept)	<b>3.9143</b>	<b>3.3072</b>	<b>4.5776</b>	<b>&lt;0.001</b>
	Trial	0.2365	0.0153	0.5214	0.0681
	Stim.Sp.Nf	-0.2791	-0.8586	0.2966	0.3527
	Stim.Sp.Sa	<b>-0.6649</b>	<b>-1.3467</b>	<b>-0.0394</b>	<b>0.0441</b>
	Stim.Sp.Sm	-0.4785	-1.0929	0.1463	0.1142
OFF	(Intercept)	-1.5877	-4.1103	0.7777	0.1920
	Trial	-0.2346	-1.3847	0.8304	0.6170
	Stim.Sp.Nf	0.5557	-1.6305	3.2308	0.6330
	Stim.Sp.Sa	-0.5857	-3.1478	2.7950	0.6690
	Stim.Sp.Sm	0.7858	-1.8002	3.1352	0.5090
<i>Sorex minutus</i>					
HAB	(Intercept)	<b>3.4070</b>	<b>2.8088</b>	<b>4.0998</b>	<b>&lt;0.001</b>
	Trial	-0.0361	-0.3339	0.3093	0.8020
	Stim.Sp.Nf	0.2377	-0.4184	0.8856	0.4310
	Stim.Sp.Sa	-0.0478	-0.7049	0.5886	0.8320
	Stim.Sp.Sm	0.2533	-0.5570	1.1643	0.5550
ENC	(Intercept)	<b>4.6578</b>	<b>4.2204</b>	<b>5.0359</b>	<b>&lt;0.001</b>
	Trial	-0.0804	-0.2684	0.0927	0.3370
	Stim.Sp.Nf	-0.2248	-0.5888	0.1072	0.1940
	Stim.Sp.Sa	-0.1427	-0.4810	0.2277	0.3950
	Stim.Sp.Sm	-0.2161	-0.7126	0.2535	0.3750
OFF	(Intercept)	<b>-2.6119</b>	<b>-5.5922</b>	<b>-0.3309</b>	<b>0.0040</b>
	Trial	0.1251	-0.8854	1.1160	0.8076
	Stim.Sp.Nf	-0.3515	-3.1748	2.4394	0.7856
	Stim.Sp.Sa	0.7885	-1.6107	3.4301	0.5190
	Stim.Sp.Sm	1.2371	-2.1532	4.2156	0.3587

Posterior means, 95% confidence intervals and probability values (PMCMC) are given. Model estimates are shown in bold when the confidence intervals do not overlap 0. HAB = activity during habituation phase, ENC = activity during encounter phase, OFF = offensive behaviour. Nf = *Neomys fodiens*, Sa = *Sorex araneus* and Sm = *Sorex minutus*. Estimates for particular species denote change relative to tests with *N. anomalus* as a stimulus species.

intensified by interspecific competition. *Neomys anomalus* lives in a marginal niche between *N. fodiens* and *S. araneus* (Rychlik, 2000, 2005). *Neomys fodiens* competes with *N. anomalus* for aquatic food resources and dominates *N. anomalus* both numerically and behaviourally (Krushinska & Rychlik, 1993; Mendes-Soares & Rychlik, 2009). *Sorex araneus* competes with *N. anomalus* for terrestrial resources and dominates it numerically (Rychlik, 2005), but not behaviourally (Rychlik & Zwolak, 2006). Living in the marginal niche between two abundant species of competitors, *N. anomalus* might indeed be faced with more limited space and food, resulting in stronger intraspecific competition. Thus, interspecific competition can be suggested as an additional factor promoting the need for *N. anomalus* to evolve individual differences in behaviours. Nevertheless, the increased number of within-group conflicts and social interactions in this species, which, according to our results, lead to consistent individual differences in behaviour, might ultimately be based on stronger intraspecific competition.

Another possible mechanism promoting the stronger interindividual differences in *N. anomalus* might be connected with their intermediate size. In their natural habitat, certain individuals of *N. anomalus* might have more experience with the larger *N. fodiens* and others with the smaller *S. minutus*. Interactions with larger shrews are more likely to end in 'losing' and interactions with smaller shrews are more likely to end in 'winning'. Such prior experiences have been shown to change future behaviour via the winner and loser effects, where winners become bolder and losers shyer (Frost, Winrow-Giffen, Ashley, & Sneddon, 2007; Hsu & Wolf, 1999). However, *S. araneus* are of intermediate size and they might also have different experiences by having, for example, encountered more of the larger *N. fodiens* or the smaller *S. minutus* in the past. Despite this, we did not find individual personality differences in social behaviour in *S. araneus*. So, even if this mechanism might have some influence, it does not seem to be the main factor in the development of personality differences in *N. anomalus*.

#### Most Species Show Consistent Individual Differences in Activity

In addition to agonistic behaviour, we also tested for consistent individual differences in activity. Not only the more sociable *N. anomalus* but also *N. fodiens* and *S. araneus* exhibited consistent individual variation in activity, as evidenced by the high levels of individual repeatability in these parameters.

Activity is a very basic behavioural trait of animals and individual differences in this trait are very common (Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson et al., 2004), including shrews (Buchalczyk, 1972; von Merten & Siemers, 2012). These differences are often related to individual differences in body mass (Saarikko, 1992), physiology and life history strategy (Careau, Bininda-Emonds, Thomas, Reale, & Humphries, 2009). Even though levels of activity are often correlated with other personality traits such as boldness or aggression, its basic nature and strong connection to physiology might explain the consistent individual differences in all our tested species and might be part of a pace-of-life syndrome (Réale et al., 2010). Fittingly, activity in the habituation and the encounter phase were positively correlated for individuals of all species (see next section).

In activity during the habituation phase *N. anomalus* showed individual differences not only in the average level of activity (individual differences in intercept) but also in the change of activity over trials (individual differences in slope). We discuss this further in the section 'Context Influences the Behaviour of Most Tested Species'.

### All Tested Species Show Correlations between Activity in Different Contexts

In all species, activity was positively correlated between the two phases: the habituation phase, when the experimental set-up was new to tested individuals and they had time to explore it on their own and the encounter phase, when habituated individuals encountered an unknown shrew of the same or a different species. This correlation was stronger in *N. anomalus* and *S. minutus* than the other two species.

Behavioural correlations across functionally unrelated contexts have been connected with animal personality: while independent behavioural responses according to differing contexts might allow for more adequate responses and should thus be favoured, several studies have shown that seemingly unrelated behaviours are often, although not always, correlated among each other, in so-called behavioural syndromes (reviews and models: Bell & Sih, 2007; Dingemanse et al., 2007; Drent, van Oers, & van Noordwijk, 2003; Sih, Bell, & Johnson et al., 2004; Wolf, van Doorn, Leimar, & Weissing, 2007).

One of the most commonly studied examples of a behavioural syndrome is the correlation between boldness and aggression (e.g. Barnett, Thompson, & Sakaluk, 2012; D'Amore, Rios-Cardenas, & Morris, 2015; Dingemanse et al., 2007). Other behavioural syndromes include correlations between activity and aggression (e.g. Kelley, Humphries, McAdam, & Boutin, 2015) or between activity and boldness, and activity and social behaviour (e.g. McCowan & Griffith, 2015). The behavioural parameters measured in our study included activity and agonistic behaviour. Both these parameters are among the five most common categories of animal personality research (see Réale et al., 2007). Here, within-individual correlation was high both across trials of activity and across trials of offensive behaviour, making them good measures for the analysis of consistent individual differences.

However, we found a correlation between activity and agonistic behaviour only in *N. fodiens*: more active individuals showed more offensive behaviour than less active ones. This result is probably a consequence not of different personality types, but rather of the general behavioural type of the species: low activity of *N. fodiens*, compared with *Sorex* species, has been described before (Buchalczyk, 1972; Lardet, 1988) and can be related to its lower metabolic rate than in the other three species (Taylor, 1998) and its general strategy of reduced activity for energy saving (Hanski, 1985). We thus assume that most of its activity during the encounter phase was offensive behaviour, which then resulted in a correlation between activity and offensive behaviour. The other three species are generally more active and thus not all their activity is spent on agonistic actions, but also on general movements such as exploration.

### Context Influences the Behaviour of Most Tested Species

*Neomys anomalus* increased their activity with an increasing number of trials in both phases of the experiment. Several partly opposing forces such as fear, curiosity or energy saving can lead to complex temporal patterns of activity in open-field tests. Their net effect (increase, decrease or no change in activity in consecutive trials) depends on the species (Archer, 1973) or strains (Bolivar, Caldarone, Reilly, & Flaherty, 2000). Most commonly, animals decrease their activity in open-field tests over repeated exposures (Archer, 1973; Martin & Réale, 2008), a phenomenon usually referred to as habituation (Shettleworth, 2009) and interpreted as a very simple form of learning. However, species tested in this study either did not change their activity levels (*N. fodiens*, *S. araneus* and *S. minutus*) or increased their activity (*N. anomalus*).

An increase in activity in repeated open-field tests (e.g. van Oers, Klunder, & Drent, 2005) is often explained by a gain in confidence. Fear is considered to inhibit exploratory behaviour in novel situations (Russell, 1973), so as some individuals of *N. anomalus* got more used to the experimental situation, they probably felt more secure about exploring the terrarium.

The size of the opponents plays a crucial role in asymmetric contests and the smaller species should be less willing than larger ones to escalate conflicts (Maynard Smith & Parker, 1976; Persson, 1985). In fact, it has also been observed among shrews that smaller species usually try to avoid conflicts or display ritualistic, not direct aggression (Kalinin et al., 1998). In contrast, equal opponents are more likely than asymmetric ones to escalate aggressive interactions (Maynard Smith & Parker, 1976; Young, 2003). Consistently with these relationships, both *Neomys* species adapted the level of their offensive behaviour to the encountered species. *Neomys fodiens* exhibited more offensive behaviour when meeting *N. anomalus* or members of the own species than when encountering either of the two *Sorex* species. The two smaller *Sorex* species seem to pose no threat to the largest tested shrew, *N. fodiens*. *Neomys anomalus* had the highest levels of offensive behaviour when encountering members of their own species or individuals of the similar sized *S. araneus*. This can probably be explained by the strong competition between these two species. The outcome of a combat with the much smaller *S. minutus* and the larger *N. fodiens* might be more obvious and the energy cost of a fight can be avoided. With similar sized individuals, however, a fight might be an important and necessary mechanism in territorial disputes, resource partitioning and niche separation.

### Conclusion

We had hypothesized that for a social species it might be adaptive to adopt a specific social niche and behave in accordance with it in different situations. Indeed, this is what we observed in the more sociable *N. anomalus*: different individuals seemed to occupy a specific social niche that they stuck to in different social contexts. According to the social niche specialization hypothesis, repeated social interactions between individuals can generate behavioural differences between them and reinforce behavioural consistency within individuals. In a species that has more frequent social interactions, the decision of who is generally more dominant and who is generally more subordinate has to be solved more often. Consequently, different personality types should be more likely to develop in a social species than in nonsocial species. We demonstrated that, in accordance with theoretical suggestions (Bergmüller & Taborsky, 2010), in a group of closely related species the most social one also has the most pronounced personality differences. *Neomys anomalus* is certainly not the most social mammal. However, considering its close relationship to the strictly solitary *N. fodiens* and the two *Sorex* species, it is striking that *N. anomalus* is indeed the one that shows the strongest tendencies for different personality types. Our results are thus an important step in understanding how social niche specialization can promote animal personality differences. Our sample size of four species is relatively small, and we encourage future studies to validate the link between social niches and personality, ideally in a taxon with a wide spectrum of sociability in multiple closely related species.

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## Supplementary Material

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