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

Sophie von Merten, Rafał Zwolak, Leszek Rychlik*

Department of Systematic Zoology, Institute of Environmental Biology, Adam Mickiewicz University, Poznań, Poland

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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.

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

* Correspondence: L. Rychlik, Department of Systematic Zoology, Institute of Environmental Biology, Adam Mickiewicz University, Umultowska 89, Collegium Biologicum, 61-614 Poznań, Poland.
E-mail address: lrychlik@amu.edu.pl (L. Rychlik).

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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, & Cowlishaw, 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)[1]	Habitat[2]	Foraging mode[3]	Sociability[4]
Neomys fodiens	14.4	Adjacent to water	Aquatic (diving and wading) and terrestrial (epigeal and hypogeal)	Solitary
Neomys anomalus	9.8	Close to water	Aquatic (mainly wading) and terrestrial (epigeal and hypogeal)	Gregarious
Sorex araneus	7.4	Rather wet, usually several metres away from water	Only terrestrial (mainly hypogeal, also epigeal)	Solitary
Sorex minutus	2.8	Rather wet, often close to water	Only terrestrial (mainly epigeal, also scansorial)	Solitary

[1] Mean body masses of animals tested in this study.
[2] Rychlik (2000).
[3] Churchfield and Rychlik (2006); Rychlik (1997).
[4] Krushinska and Rychlik (1993, 1998).