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# Exploration and sociability in a highly gregarious bird are repeatable across seasons and in the long term but are unrelated



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Keywords: animal personality behavioural syndrome (co)variance partitioning long term seasonal context social behaviour Sturnus vulgaris Personality traits and behavioural syndromes are often assumed to relate to life history strategies and lifetime fitness variation and hence may be generally under selection. Key in this regard is the, often untested, assumption that individual differences in (correlated) behaviours are maintained across contexts and over an individual's lifetime. Here, we tested this assumption, using a population of 30 captive male starlings, Sturnus vulgaris, a highly gregarious avian species. We repeatedly assayed novel environment exploration and different aspects of sociability towards a female conspecific, across seasonal contexts (spring and autumn) and across a 2-year period, which represents a substantial portion of a starling's life span. We found that, regardless of plasticity at the population level, both exploration behaviour and sociability traits investigated were moderately repeatable across seasons and years, with no significant differences between repeatability estimates over different timescales. However, no evidence was found for significant between-individual correlations between the investigated traits, including different aspects of sociability. Taken together, our results provide empirical evidence that exploration and sociability are personality traits that are stable across seasons and in the long term but do not form behavioural syndromes. Given the recent evidence that personality traits are often heritable, the traits assessed in our study might have the potential to evolve independently under selection. This long-term consistency in exploration and sociability might have important implications for the social organization within complex social environments and influence a wide variety of ecologically relevant processes.

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Across a variety of animal taxa, individuals within populations often display remarkable differences in behavioural tendencies that are consistent across time and contexts (Gosling, 2001; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson, 2004). Such consistent (i.e. repeatable) individual differences in average behaviour are referred to as 'personality' (Dingemanse, Kazem, Réale, & Wright, 2010; Garamszegi & Herczeg, 2012), and different personality traits are often observed to covary between individuals, forming so-called behavioural syndromes (Sih et al., 2004). However, behaviour is inherently plastic and thus (co)varies within individuals (Bell, Hankison, & Laskowski, 2009; Dingemanse et al., 2010). One therefore needs to partition the raw phenotypic (co)variation, from repeated measurements on individuals, into its within- and between-individual components (see Dingemanse & Dochtermann, 2013).

Despite increasing research interest, explaining the existence and maintenance of personality variation remains puzzling (e.g. Dingemanse & Wolf, 2010; Réale, Dingemanse, Kazem, & Wright, 2010). Nevertheless, growing evidence suggests that personality traits are heritable, linked with life history traits and lifetime fitness variation (e.g. Biro & Stamps, 2008; Dochtermann, Schwab, & Sih, 2015; Smith & Blumstein, 2008), and hence might be maintained by life history trade-offs (e.g. Wolf, Van Doorn, Leimer, & Weissing, 2007). These observations have been integrated into the pace-oflife syndrome (POLS) hypothesis, suggesting the coevolution of physiology, personality and life history (Réale, Garant, et al., 2010). However, if long-term selection results in the coevolution of personality and life history traits, one key assumption is that individual differences in (correlated) behaviours are maintained over considerable portions of a species' lifetime (Brommer & Class, 2015; Réale, Garant, et al., 2010; Stamps & Groothuis, 2010). Similarly,

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these individual differences are expected to be maintained across ecologically relevant contexts (e.g. predation pressure, photoperiod or reproductive seasons; Dingemanse et al., 2010). To date, surprisingly little is known about the extent to which consistent behavioural differences are maintained across seasons and over long periods of time (but see Class & Brommer, 2015; David, Auclair, & Cézilly, 2012; Kluen & Brommer, 2013; Wuerz & Krüger, 2015). Explicitly addressing these questions is crucial, ultimately because they have important implications for our understanding of the development, ecological significance and evolutionary potential of personality traits and behavioural syndromes (Brommer & Class, 2015; Réale, Dingemanse et al., 2010; Réale, Garant, et al., 2010; Stamps & Groothuis, 2010).

One behavioural trait commonly found to be consistent is exploration behaviour in a novel environment (e.g. great tits, Parus major: Dingemanse, Both, Drent, van Oers, & Van Noordwijk, 2002; European starlings, Sturnus vulgaris: Minderman, Reid, Evans, & Wittingham, 2009; zebra finches, Taeniopygia gutatta: Schuett & Dall, 2009; house sparrows, Passer domesticus: Mutzel, Kempenaers, Laucht, Dingemanse, & Dale, 2011; fairy-wrens, Malurus cyaneus: Hall et al., 2015). This aspect of personality is often observed to be part of a behavioural syndrome including boldness, activity and aggression (see Garamszegi, Marko, & Herczeg, 2013). Another trait termed sociability, defined as an individual's nonaggressive behavioural response to conspecifics, might also constitute an aspect of personality (Réale et al., 2007). In highly gregarious species, sociability refers to a broad trait category encompassing a range of social behaviours (e.g. tendency to seek proximity to conspecifics, sexual behaviour towards opposite-sex conspecifics, affinitive behaviour, etc.: Cote & Clobert, 2007; Koski, 2011; Schuett & Dall, 2009). Despite growing interest in the influence of the social environment on personality, and vice versa (see Webster & Ward, 2011; Wolf & Krause, 2014), studies investigating which types of social behaviour represent aspects of personality are limited (but see Aplin et al., 2015; Cote & Clobert, 2007; Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010; Koski, 2011). Insights into the consistency of individual differences in sociability are important, especially in gregarious species (see Koski, 2014), since they are likely to play an important role in interactions within complex social environments, might be shaped by sexual selection under certain conditions, and might influence behavioural strategies and ultimately fitness (e.g. Cote, Dreiss, & Clobert, 2008; Farine & Sheldon, 2015; Formica et al., 2012; McGhee & Travis, 2010; Oh & Badyaev, 2010). Consistent individual differences in sociability are hence expected to be integrated within a general pace-of-life syndrome (POLS); with slow, more thorough explorers being on average more social than fast, superficial explorers (Réale, Garant, et al., 2010). To date, this specific relationship largely remains untested (Budaev, 1997; Haage, Bergvall, Maran, Kiik, & Angerbjörn, 2013; McCowan, Mainwaring, Prior, & Griffith, 2015).

Here, we integrated some largely overlooked aspects and hypotheses in the personality literature using the European starling, a highly gregarious hole-nesting species with complex social behaviour (Eens, 1997; Feare, 1984). Specifically, we (1) integrated different aspects of sociability (time spent near a female conspecific and near the provided nestbox in the presence of a female), in addition to novel environment exploration behaviour, within a personality framework and (2) tested the POLS hypothesis' proposed negative relationship between exploration and sociability traits (Réale, Garant, et al., 2010). Simultaneously, we explicitly investigated (3) whether behavioural repeatability and behavioural syndrome structure between these traits varied across seasonal contexts (spring and autumn) and/or across years. If betweenindividual differences in (correlated) behaviours are maintained across seasons and years this would suggest their (correlated) evolutionary response to selection.

# **METHODS**

# Ethical Note

All experiments undertaken in this study complied with ethical guidelines of the University of Antwerp and Flemish and European laws regarding animal welfare, and adhere to the ASAB/ABS guidelines for the use of animals in behavioural research and teaching. Specifically, permission to capture starlings from the wild and house them in captivity (in approved facilities) was granted by the Flemish administration (Agentschap voor Natuur en Bos, ID numbers ANB/BL-FFN 08-11344 and ANB/BL-FFN 12-00381). Behavioural assays were approved by the ethical committee of the University of Antwerp (ID number 2011-31). Neither procedure adversely affected the starlings in the short term or for the overall period of the study. After each test session (see below), birds were returned to their holding conditions.

# Subjects

Thirty juvenile males, judged from their plumage characteristics (Svenson, 1984), were caught from the wild at several sites around Antwerp, Belgium (51°13'N, 4°24'E), in October 2008. From then onwards all males were held captive under the same standardized conditions in a single large outdoor aviary (16 × 6 m and 2.5 m high) equipped with several perches, at the University of Antwerp campus in Wilrijk, Belgium. Starlings can be kept easily in captivity, where they show normal social and reproductive behaviour (Eens, Pinxten, & Verheyen, 1990; Eens, Pinxten, & Verheyen, 1993). Upon introduction into this aviary, males were ringed with a numbered metal ring and a unique combination of plastic colour rings, allowing easy identification. Food (mixed 1/3 Orlux UniPatee, Orlux, Belgium and 2/3 Merelkorrel Speciaal, Nifra–Van Camp, Belgium) was provided ad libitum, and birds had unrestricted access to drinking and bathing water.

#### Test Room

The test room (Fig. 1) was a modified version of one used to quantify exploration behaviour in great tits (Dingemanse et al., 2002; Verbeek, Drent, & Wiepkema, 1994). It was a wooden structure ( $2.95 \times 2$  and 2.5 m high) with a closed roof, three blind white walls and wire-mesh front wall. A wooden 'start box'  $(24 \times 14 \text{ cm and } 14 \text{ cm high})$  was connected to the test room via an entrance hole (diameter = 5 cm) at a height of 1.6 m, allowing birds to enter the room without further handling. Inside the test room there were nine 'items': five perches, a shelf, a food dish, a small cage and the wire mesh. A small wire cage ( $24 \times 16$  cm and 22 cm high) next to perch 4 was present for the sociability assay (see below). Furthermore, a nest hole (diameter = 5 cm) at a height of 1.1 m, close to perch 5, was connected to a nestbox attached at the outside of the room. Given that starlings also explore the ground during exploration tests (Minderman et al., 2009), the ground was covered with sand and provided with two strips of grass  $(2.95 \times 0.4 \text{ m})$ , one on each side, dividing the ground into three distinct parts. Observations were made by a single observer in a darkened hide behind a one-way screen and all trials were videotaped (Sony Handycam HDR-XR550E/XR550VE).

# Behavioural Assays

#### General procedure

Over a 2-year period (2011 and 2013), all males took part in four exploration trials and three sociability trials (Table 1), and were kept and handled in the same standardized conditions. Two days

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