



Exploration behaviour in a different light: testing cross-context consistency of a common personality trait



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Laboratory measures of personality traits are often used to answer both evolutionary and ecological questions involving behavioural variations in the wild within and between populations. However, little is known about the actual behavioural mechanisms behind any correlation with behaviours in the wild, and traits often lack validation in a different context. We examined whether the commonly used exploration behaviour trait constitutes an active exploration strategy, by testing whether the activity in the exploration test could also be captured in a different exploration context. We subjected great tits, *Parus major*, to two different tests, one being the standardized exploration behaviour test and one a newly constructed test. The new test arena contained eight large rooms connected by corridors, where we scored the activity of individuals and the number of rooms visited as a proxy for exploration. We found that our new exploration test captured repeatable behaviour in activity and exploration of rooms both within and across years. We found no correlations between the two tests, suggesting that they may not capture the same behaviour, in terms of exploration of rooms or activity. We conclude that in our study population, the classic exploration behaviour test seems context specific, rather than constituting a general exploration strategy.

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Consistent between-individual variation in behaviour, most commonly defined as animal personality (Gosling, 2001; Sih, Bell, & Johnson, 2004) or temperament (Gosling, 2001), is a widely studied topic from both an evolutionary and ecological perspective (Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Wolf & Weissing, 2012). Animal personality is normally considered a set of several underlying personality traits such as aggression (Arya-Ajoy & Dingemans, 2014; Huntingford, 1976), activity (Gosling, 2001) and exploration (Verbeek, Drent, & Wiepkema, 1994). These traits are typically quantified by their expression under standardized laboratory conditions and are commonly related to a number of behaviours and life history traits in the wild (Reale, Dingemans, Kazem, & Wright, 2010). Findings of such relationships support the idea that animal personality plays a central role in population dynamics and micro-evolution (Clobert, Baguette, Benton, & Bullock, 2012; Dochtermann & Dingemans, 2013; Wolf & Weissing, 2012).

Currently, there is a gap of knowledge in how behaviours quantified in an artificial laboratory setting, often in small test environments with minimal complexity such as test cages and test rooms, translate to behaviour in larger and more complex environments as an intermediate step to the wild. There are several important reasons to study this question. One is that selection ultimately acts on the expression of personality traits in the wild, and not on behaviour measured in a laboratory setting. Another equally important reason is that there is little understanding of what behaviours are actually measured in captivity. The importance of validating the meaning of behavioural traits has been emphasized recently (Carter, Feeney, Marshall, Cowlshaw, & Heinsohn, 2013; Niemela & Dingemans, 2014). This is particularly important in scenarios in which a behavioural trait measured in a single captive context is used to draw conclusions about different behaviours in the wild, or when an empirical correlation is found between a laboratory trait and a presumed different behaviour in the wild. The difficulty in understanding a personality trait's functional meaning makes cross-context validations of behavioural measures necessary, which has been referred to as convergent validity (Carter et al., 2013). One way to validate a laboratory measure is to correlate measures of behaviour that are presumed to measure the same

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trait, or closely linked traits, in captivity and the wild. In great tits, *Parus major*, for example, Morand-Ferron and Quinn (2011) found that individual problem-solving capacity in captivity was correlated with problem solving at a feeder study during winter. Herborn et al. (2010) assayed both exploration behaviour and neophobia in blue tits, *Cyanistes caeruleus*, and found correlations between these two traits in captivity and their analogues in the wild. Many laboratory-measured traits still need cross-context validation, however, and more work is needed to understand how behaviours expressed in standardized environments correlate with behaviour in other environments (Niemela & Dingemanse, 2014).

A common measure of personality used in a wide range of animal species is the rate at which an individual moves through a novel space, normally referred to as 'exploratory behaviour' or 'exploration' (Dingemanse, Both, Drent, Van Oers, & Van Noordwijk, 2002; Reale, Reader, Sol, McDougall, & Dingemanse, 2007; Verbeek et al., 1994). It is often measured in a single non-subdivided space with few structures and is assumed to reflect an underlying 'exploration trait' which can only be expressed in a novel environment (Reale et al., 2007). Correlations have been found between individual variation in exploration behaviour and other behaviours including foraging routines (Verbeek et al., 1994), risk-taking behaviour (van Oers, Drent, de Goede, & van Noordwijk, 2004), antipredator behaviour (Jones & Godin, 2010) and aggression towards conspecifics (Carere, Drent, Privitera, Koolhaas, & Groothuis, 2005; Wilson et al., 2009). Exploration behaviour has been shown to be heritable within several taxa such as fish (Dingemanse et al., 2009), mammals (Careau et al., 2011; Kanda, Louon, & Straley, 2012) and birds (Dingemanse et al., 2002; Korsten et al., 2010; Quinn, Patrick, Bouwhuis, Wilkin, & Sheldon, 2009). As it is measured as a response to a novel environment, exploration behaviour has often been predicted to play a role in spatial movement in the wild (Cote, Clobert, Brodin, Fogarty, & Sih, 2010), and multiple studies have found correlations between exploration behaviour and expressions of spatial behaviour such as dispersal distance (Dingemanse, Both, van Noordwijk, Rutten, & Drent, 2003; Fraser, Gilliam, Daley, Le, & Skalshi, 2001; Hoset et al., 2010; but see Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010), seasonal dispersal movements (Chapman et al., 2011; Thijs van Overveld, Careau, Adriaensen, & Matthysen, 2014), home range sizes (Minderman, Reid, Evans, & Whittingham, 2009; van Overveld, Adriaensen, & Matthysen, 2011) and family movements (van Overveld et al., 2011). A recent study found evidence for a genetic integration of heritable variation in both exploration behaviour and dispersal distance (Korsten, van Overveld, Adriaensen, & Matthysen, 2013). Exploration behaviour thus reflects a personality trait that can be a target of selection associated with spatial behaviours, and is therefore an informative trait for examining individual and population level processes in behavioural and movement ecology (Cote, Clobert, et al., 2010; Sih et al., 2012).

Despite the accumulating evidence that exploration behaviour correlates with spatial behaviours, the way in which variation in exploration behaviour translates into these behaviours is still not clear. An obvious candidate behavioural mechanism is that individual variation in exploration behaviour directly translates into larger-scale spatial movements in the wild through variation in exploration strategies. Differences in the intensity, willingness or thoroughness of exploration may result in significant between-individual variation in spatial displacement over time. If exploration behaviour indeed reflects a general strategy of exploring unknown environments, in the laboratory as well as in the wild, then we would expect variation in exploration behaviour to be highly consistent across contexts that vary strongly in spatial scale and complexity. In this study we tested this hypothesis by measuring individual exploration behaviour in two different laboratory based

contexts: a standardized exploration behaviour test that is widely used in our focal species by several different research groups and a newly constructed test involving a larger space and more complex environment. The alternative hypothesis is that the link between spatial behaviours and exploration behaviour is caused by covariation between exploration behaviour and other behaviours that do not directly involve exploration, such as aggressiveness and dominance (Adriaenssens & Johnsson, 2010b; Dingemanse, 2004) or differences in use of social information (Aplin, Farine, Mann, & Sheldon, 2014), which we did not address in this study. Additionally, underlying differences in physiology such as metabolic rate could also cause differences in spatial movements through differences in general activity levels (Biro & Stamps, 2008).

Few previous studies have tried to relate exploration behaviour measures across contexts. A study in crickets (Dochtermann & Nelson, 2014) found no evidence for cross-context consistency. Herborn et al. (2010) tested relationships between discovery of new feeders in the wild and activity in a captive novel environment, but found no relationship. When they instead used a residual measure for exploration behaviour by subtracting activity in a known environment from the activity in the novel environment, they found a significant relationship with exploration behaviour in the wild. It has already been noted that individual variation in activity might interfere with the measure of exploration (Reale et al., 2007). Therefore we aimed at quantifying different behaviours that might reflect either activity or exploration behaviour expressed in activity and additionally exploration behaviour in terms of forward movement. We used two different tests for this: the standardized exploration behaviour test which quantifies the activity in a novel but limited environment, where the measurement is referred to as the exploration behaviour score, and a newly constructed test which quantifies both the activity and forward movement in an equally novel, but more complex environment.

We used the great tit as a model species. In this species, variation in exploration behaviour in a small novel room has been studied in great detail and has been replicated in many populations since the early 1990s (Dingemanse et al., 2002; Hollander, Van Overveld, Tokka, & Matthysen, 2008; Quinn et al., 2009; Verbeek et al., 1994). Several studies have confirmed the repeatability of the exploration behaviour score, as well as showing similar responses to test conditions such as test sequence or time elapsed between tests (Dingemanse et al., 2012; Korsten et al., 2013; Quinn et al., 2009).

We designed a new laboratory based exploration test, named the arena test, in which we challenged great tits to explore a more complex novel environment composed of several connected rooms. In addition to quantifying activity within a room, the arena also gives the option of forward movement through the set of rooms as opposed to the exploration behaviour test. By this design we hoped to be able to differentiate between two behavioural responses that may or may not reflect variation from the same assumed latent 'exploration trait': activity as measured by number of movements and forward movement as the number of rooms visited. We refer to these proxies as 'Arena Activity' (total number of movements within all rooms) and 'Rooms Visited' (forward exploration of rooms).

In this paper, we use 'exploration behaviour' as an overall term for behaviours observed in novel room tests such as the exploration behaviour test. The quantified behaviour from the standardized exploration test is referred to as the exploration behaviour score. From the newly constructed exploration test, the arena, we quantified two variables: Arena Activity and Rooms Visited. Arena Activity was measured similarly to the exploration behaviour score with total number of movements within the tests, whereas Rooms Visited was the number of rooms a bird visited, only possible through forward movement.

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