



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



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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-of-life 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; Klun & 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 guttata*: 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, affiliative 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 between-individual 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 × 2 and 2.5 m high) with a closed roof, three blind white walls and wire-mesh front wall. A wooden 'start box' (24 × 14 cm and 14 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 × 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 × 0.4 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

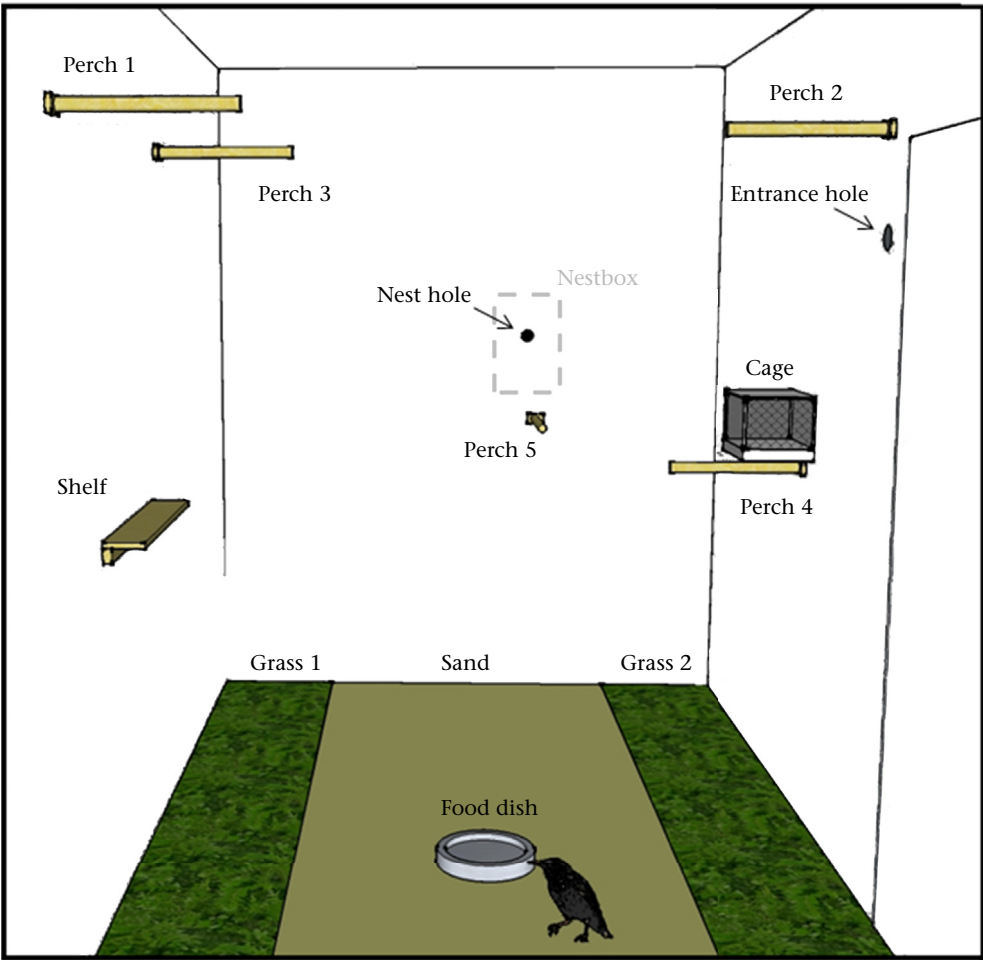


Figure 1. Schematic overview of the test room. The entrance hole in the test room was connected to the start box and the nest hole was connected to a nestbox both attached on the outside of the room (marked in grey). The wire-mesh front wall is not depicted.

before the start of each session, all males were caught from the large aviary and randomly allocated to six identical smaller outdoor aviaries (3.2×2 m and 2.5 m high), where they were housed in groups of five and provided with food and water ad libitum. The day before the behavioural assays, all birds from each small aviary were weighed and transported to individual cages (100×30 cm and 40 cm high), located in two separate outdoor aviaries, identical to the small outdoor aviaries in which they were housed. The next day, each bird was caught from his individual cage (random but alternately between aviaries) and placed in the completely opaque start box connected to the test room (Fig. 1).

Exploration assay

After the male had spent 5 min in the start box for acclimatization, the entrance hole giving access to the test room was opened

by lifting a slide and the time it took the bird to enter the room (latency) was recorded. If the bird had not entered the test room by itself (spontaneous enter) after 1 min, it was encouraged to do so by briefly lifting the outside entrance of the start box (forced enter), and subsequently appointed a maximum latency of 60 s. As males either spontaneously entered within 10 s (52% of the trials) or had a maximum latency of 60 s (36% of the trials), latency was transformed into a binary variable (i.e. spontaneous versus forced enter).

The exploration trial started once the bird entered the room and lasted for 15 min, during which the following behavioural parameters were recorded (see also Minderman et al., 2009): (1) number of unique items visited (maximum 12, see Fig. 1) (2) total number of visits to items and (3) total number of flights. As, in contrast to Minderman et al. (2009), the observed variation in the time spent on the ground was low in our study population, and particularly

Table 1
Overview of data collection

Year	Season	Session	Date	Exploration	ITI (expl)	Sociability	ITI (soc)
2011	Spring	1	6–14 April	Trial 1	11±1	Trial 1	174±3
		2	19–24 April	Trial 2			
		3	27 April–3 May				
	Autumn	4	19–22 October	Trial 3	182±3	Trial 2	
2013	Spring	5	11–16 April	Trial 4	542±7	Trial 3	542±7

ITI is intertrial interval in days (mean ± SD) between consecutive trials of exploration (expl) and sociability (soc) assays.

during the first trial (with only one male visiting the ground), we scored the different parts of the ground (i.e. grass 1, grass 2 and sand; Fig. 1) as three additional items and not as separate exploration parameters.

Sociability assay

Sociability trials immediately followed the 15 min exploration trials, except in spring 2011 when the sociability trial followed approximately 7 days after the second exploration trial (Table 1). However, males were allowed to explore the room for 5 min preceding the sociability trial in spring 2011. In total, 13 different stimulus females were used, i.e. three, four and six different females for trial 1, 2 and 3, respectively. The same female was never used for two consecutive trials on the same day. Sociability trials started by dimming the light in the test room and placing a single stimulus female into the small cage via a slide from outside (Fig. 1). Trials lasted 15 min after the lights were turned on again. During these trials, behavioural parameters associated with the male's response towards female conspecifics were recorded (Eens et al., 1990, 1993; Gwinner, Van't Hof, & Zeman, 2002; Pinxten, De Ridder, & Eens, 2003): time spent in proximity to the female (Time FE) and time spent near the nestbox (Time NB).

One commonly assessed component of sociability is the tendency to seek proximity to conspecifics, referred to as 'social tendency' (e.g. Budaev, 1997; Cote & Clobert, 2007; McEvoy, While, Sinn, Carver, & Wapstra, 2015). As a measure of this tendency we quantified Time FE, referring to the sum of the time spent on the small cage in which the female was placed and on the perch near the small cage (perch 4). During the breeding season (i.e. spring), male starlings having access to a nest hole may respond to the presence of a conspecific female by showing mate attraction behaviour, i.e. trying to attract the female to this nest hole by sitting close to it, hanging in the nest hole or by entering it (Eens et al., 1993; Gwinner et al., 2002). Furthermore, during the nonbreeding season (e.g. autumn) there may be competition between (captive) starlings for access to a nest hole to roost (Pinxten, De Ridder, De Cock, & Eens, 2003). We therefore quantified Time NB, referring to the sum of the time spent hanging in the nest hole, on the perch near the nest hole (perch 5) and in the nestbox. Time NB is thus assumed to indicate the investment in mate attraction (spring) or competition (autumn) in response to the presence of the female. Moreover, including Time FE and Time NB as separate parameters allowed us to assess the relative investment in, and relation between, both measures of sociability. As we were also interested in the relation between exploration and the overall response towards a female, we included a composite measure of sociability (Time TR), calculated as the sum of Time FE and Time NB. All three measures, which we refer to as sociability traits, were expressed as proportional times, relative to the total duration of the trial.

Statistical Analyses

All analyses were performed in R 3.1.0 (R Core Team, 2014). Prior to analyses, Time NB and Time FE were square-root transformed to meet the normality of residuals assumption in linear models, and all three sociability traits were standardized (Schielzeth, 2010). The three parameters that quantified exploration were log-transformed, standardized and entered in one overall principal component analysis (PCA). This PCA resulted in a single principal component (eigenvalue = 2.85) explaining 95% of the variance, with strong positive loadings for all parameters, i.e. number of unique items visited (0.568), total number of visits to items (0.586) and number of flights (0.578). This principal component, referred to as 'Expl (PC)', was used in all further analyses as an overall measure of exploration behaviour.

Univariate mixed models

Univariate mixed models (MMs) were used to investigate the influence of potential covariates and factors on each of the behavioural traits. Separate univariate MMs were fitted (lmer function, package lme4; Bates, Mächler, Bolker, & Walker, 2014) with Gaussian error-distribution and included random intercepts for male identity (ID). Context (spring versus autumn) and year (2011 versus 2013) were included as fixed effects in all models. Furthermore, body mass and time of day were centred within individuals (van de Pol & Wright, 2009) and both within- and between-individual components were added as fixed effects in all models. The model for Expl (PC) also included the factor latency (spontaneous versus forced enter) as a fixed effect. Stepwise backward elimination of nonsignificant terms, starting with the least significant, was used to obtain minimum adequate MMs. To explore the overall effect of female identity on male response, a likelihood ratio test (LRT) between the mixed models for Time TR with and without Female ID as extra random effect was performed (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

Furthermore, because of our unbalanced sampling design (Table 1), separate univariate MMs with a random intercept for ID were used to estimate the short-term and long-term repeatability of Expl (PC). All other repeatabilities (for both exploration and sociability traits) were estimated from the multivariate MMs. The sim function (package arm; Gelman et al., 2015) was used to simulate values of the posterior distribution of all model parameters and we considered effects significant when credible intervals (CrI) did not overlap zero. Fixed effects found to be nonsignificant in the univariate MMs were omitted in further multivariate MMs.

Multivariate mixed models

To partition (co)variances we applied multivariate MMs using the MCMCglmm package (Hadfield, 2010), which relies on Markov Chain Monte Carlo sampling to estimate parameters. A prior distribution ($V = \text{diag}(4)$, $\nu = 1.004$) was used throughout, and chains were run for 1.3 million iterations, with a burn-in phase of 300 000 and a thinning interval of 1000 iterations. The use of a range of alternative prior specifications (e.g. default) did not affect the results qualitatively. Convergence and mixing of models was assessed by visually checking traces of posterior distributions over iterations and Gelman–Rubin statistics between chains (Gelman & Rubin, 1992; potential scale reduction factor <1.1 for all parameters). Autocorrelation within chains was <0.07 for all parameters (Hadfield, 2010), indicating all model assumptions were met. All multivariate analyses were run with the average of the individual PC scores of the first two exploration trials, resulting in a single exploration score per male for the spring of 2011.

We ran three multivariate MMs, using different (sub)sets of data which included the repeated measurements relevant for the period of interest, i.e. overall (three repeats), across-season (spring 2011–autumn 2011) and across-year (spring 2011–spring 2013) data sets. All models, with the four behavioural traits as response variables, were fitted assuming multivariate Gaussian error distribution and included the fixed effects found to be significant in the previously described univariate MMs. Hence, all behavioural traits, including the three sociability measures, were modelled as separate traits, but this assumption was explicitly examined by calculating the between- and within-individual correlations between them (see Baugh, van Oers, Dingemanse, & Hau, 2014 for a similar approach).

In each multivariate model we included male ID as random intercept, allowing the partitioning of the multivariate phenotypic (co)variances (not explained by the included fixed effects) into its between- and within-individual components. Adjusted repeatabilities for each of the traits were then estimated as the between-individual variance (V_i) divided by the total phenotypic

variance (i.e. sum of V_I and within-individual variance V_R ; Nakagawa & Schielzeth, 2010). Between- (COV_I) and within- (COV_R) individual covariances between pairs of traits were divided by the square-root of the product of their respective variances to obtain the corresponding between- (r_I) and within- (r_R) individual correlations, respectively (see Dingemanse & Dochtermann, 2013). All results are presented as means with 95% CrI, unless stated otherwise, and were considered significant when CrI did not overlap zero.

RESULTS

Population Level Effects

Both season and year had a significant effect on population level exploration (Table 2). Male exploration behaviour was higher in the autumn (0.64 ± 0.36 SE) than in the spring (-0.21 ± 0.16 SE) and in 2013 (0.60 ± 0.30 SE) than in 2011 (-0.20 ± 0.18 SE). However, exploration behaviour did not differ on average between the two exploration trials in the spring of 2011 (Fig. 2). Adding Female ID as random effect in the mixed model of male total response (Time TR) towards a female did not improve the fit (LRT: $\chi^2_1 = 1.99$, $P = 0.16$), and was removed from further analyses. Furthermore, male total response (Time TR) was significantly influenced by season (Table 2), with males responding on average more to the presence of the female in the autumn (0.56 ± 0.06 SE) than in the spring (0.41 ± 0.05 SE). The overall response of males, however, was not significantly different between years (Table 2, Fig. 3). The time spent near the nestbox (Time NB) was significantly influenced by both season and year (Table 2), indicating that males spent on average more time near the nestbox in the autumn (0.25 ± 0.05 SE) than in the spring (0.11 ± 0.03 SE), and in 2013 (0.18 ± 0.05 SE) than in 2011 (0.15 ± 0.03 SE; Fig. 3). On the other hand, males spent on average the same amount of time near the female (Time FE), regardless of season or year (Table 2, Fig. 3). None of the other potential covariates and factors had a significant influence on any of the investigated traits (Table 2).

Short-term, Across-Season and Long-term Repeatability

Males showed significant between-individual differences over different timescales for all four investigated behavioural traits, with season and/or year included as fixed effects in the models (Table 3). Male exploration behaviour (Expl (PC)) was consistent over short

and long time periods but repeatability was lower across seasons. For male total response (Time TR), across-season repeatability was higher than, although not significantly different from, across-year repeatability. Males differed consistently in the time they spent near the nestbox (Time NB), both across seasons and years. The time males spent near the female (Time FE) was also repeatable, with moderate to low repeatabilities across seasons and years. For all traits, the repeatability estimates did not differ significantly over different time periods and across seasons, as indicated by overlapping CrIs.

Between- and Within-individual Correlations

First, overall, exploration behaviour and sociability traits were not observed to covary over any timescale, either between or within individuals (Table 4). However, across spring 2011 and spring 2013, exploration showed a tendency to be positively correlated within individuals with both the total response (Time TR) and especially with the time males spent near the nestbox (Time NB; Table 4). This tendency between exploration and Time TR and Time NB was conserved in the overall data set, despite being attenuated by the absent across-season correlation (Table 4).

Second, the time males spent near the nestbox (Time NB) and near the female (Time FE) did not covary, either between or within individuals. The total response during the sociability trials (Time TR), on the other hand, was positively correlated both between and within individuals with the time near the nestbox and the time near the female (Table 4).

DISCUSSION

We found that novel environment exploration and different aspects of sociability were moderately repeatable across seasons and a 2-year period, representing a substantial part of the adult starling's life span (Feare, 1984). Regardless of population level plasticity for some traits, repeatability estimates did not differ across timescales, indicating that these personality traits are stable in male starlings. However, we found no evidence for significant between-individual correlations (i.e. behavioural syndromes) between exploration and the sociability traits. Moreover, different aspects of sociability did not covary between individuals, and appeared to be independent aspects of male starlings' social personality. In what follows, the potential ecological and evolutionary implications of our findings are discussed.

Table 2
Output of univariate mixed models for the total data set of the four behavioural traits

	Expl (PC)	Time TR	Time NB	Time FE
Fixed effects				
Intercept	-0.62 (-1.06; -0.15)	-0.15 (-0.43; 0.14)	-1.06 (-1.65; -0.47)	0.00 (-0.26; 0.26)
Season ^a	1.25 (0.72; 1.84)	0.42 (0.08; 0.76)	0.94 (0.60; 1.29)	0.22 (-0.15; 0.57)
Year ^b	1.22 (0.68; 1.78)	0.23 (-0.17; 0.63)	0.56 (0.21; 0.89)	0.00 (-0.45; 0.44)
Latency ^c	-0.50 (-1.11; 0.17)	NA	NA	NA
Time of day (b)	-1.56 (-6.74; 4.06)	2.32 (-1.86; 6.23)	-0.55 (-4.80; 3.57)	2.32 (-1.54; 6.22)
Time of day (w)	-0.64 (-4.63; 3.26)	0.34 (-2.24; 2.74)	1.80 (-0.48; 4.06)	-1.65 (-4.42; 0.93)
BM (b)	0.00 (-0.06; 0.07)	-0.03 (-0.07; 0.02)	-0.02 (-0.06; 0.03)	-0.02 (-0.07; 0.02)
BM (w)	-0.06 (-0.13; 0.02)	0.00 (-0.04; 0.05)	0.03 (-0.01; 0.07)	-0.03 (-0.08; 0.02)
Random effects				
ID	0.88 (0.56; 1.29)	0.40 (0.26; 0.59)	0.38 (0.26; 0.56)	0.31 (0.20; 0.47)
Res	1.65 (1.31; 2.16)	0.58 (0.44; 0.81)	0.49 (0.36; 0.64)	0.70 (0.52; 0.94)

Results are presented as coefficients (β) with 95% credible intervals for fixed effects and as variance components (σ^2) with 95% credible intervals for random effects. Significant results are highlighted in bold. Expl (PC) is the exploration principal component, Time NB the time spent near the nestbox, Time FE the time spent in proximity to the female and Time TR the sum of the two latter traits. (b) and (w) represent the between- and within-individual components of the fixed effects, respectively.

^a 'Spring' is used as reference category.

^b '2011' is used as reference category.

^c 'Spontaneous enter' is used as reference category.

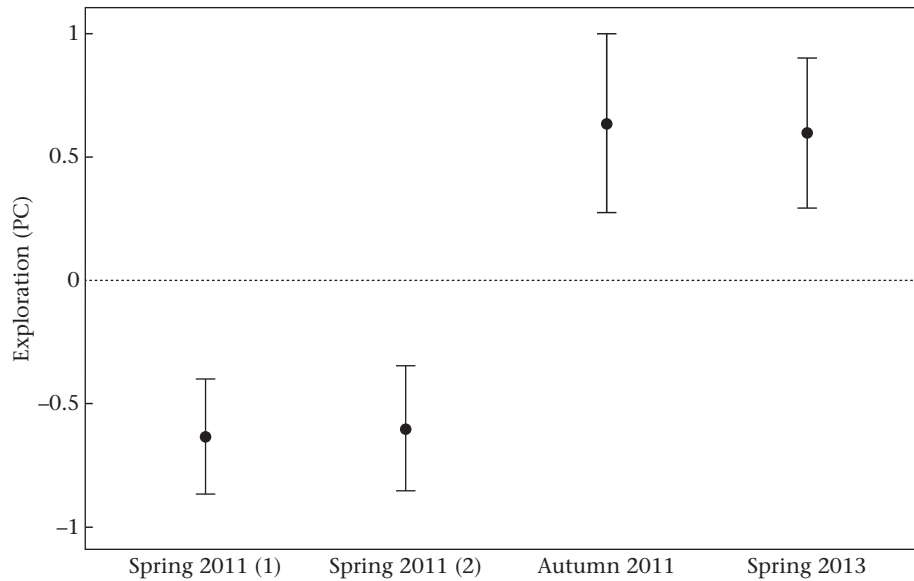


Figure 2. Exploration score (PC) per trial (mean \pm SE) for 30 male starlings. For intertrial intervals see Table 1.

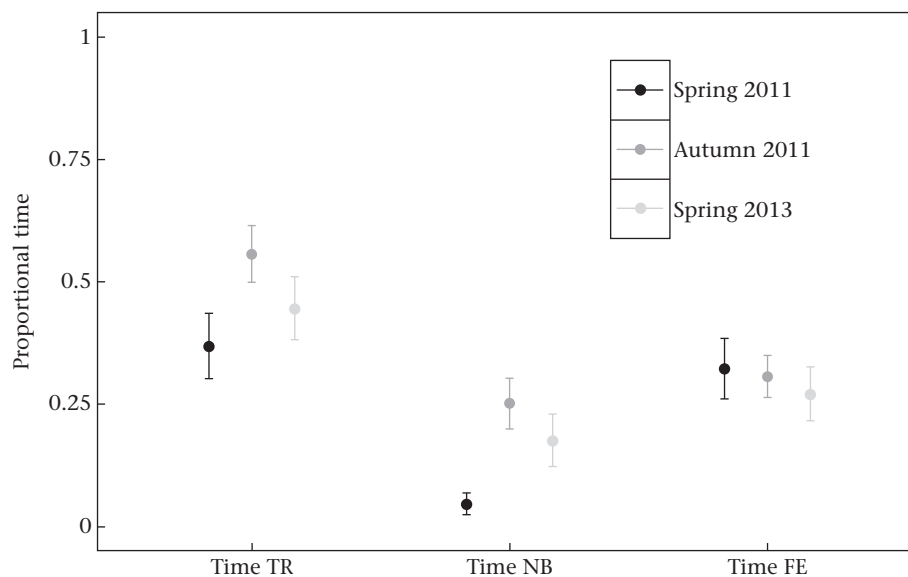


Figure 3. Proportional times (mean \pm SE) for the three sociability traits during the sociability assay over the different trials for 30 male starlings. Time NB refers to the time spent near the nestbox and Time FE to the time spent in proximity to the female. Time TR is the sum of Time NB and Time FE. For intertrial intervals see Table 1.

Population Level Plasticity Across Seasons and Years

Novel environment exploration and time spent near the nestbox increased from the spring towards the autumn of 2011 and remained at approximately the same level in the spring of 2013. The average time spent in proximity to the female did not differ between seasons and years. Several studies have reported an increase in exploration with repeated exposure to an ‘open field’ test, assumed to be caused by a reduction in fear with increased habituation (e.g. Budaev, 1997; Dingemanse et al., 2002; Minderman et al., 2009). Such habituation effects are expected to be more pronounced on shorter timescales (e.g. Dingemanse et al., 2002). Our findings are not in accordance with this explanation since exploration only increased between the trials with the longest intertrial intervals (Fig. 2). Unfortunately, data were not available (no repeated measurements within seasons and years, e.g. Boulton,

Grimmer, Rosenthal, Walling, & Wilson, 2014) to disentangle habituation and experience effects from season and year effects, and their relative contributions in explaining our results therefore remains unresolved.

One interesting possibility is that males become more exploratory and spend more time near the nestbox as they develop. Indeed, life history theory predicts that individuals take more risk and invest more in reproduction with age as their future fitness expectations decrease (e.g. Roff & Fairbairn, 2007; Stearns, 1989). Our observation that males spent more time near the nestbox in the second, relative to the first, spring is in line with these predictions (e.g. Gwinner et al., 2002). At present, this remains speculative and age-related effects at the population level (and individual/genetic level; see Brommer & Class, 2015) deserve more empirical attention (see Class & Brommer, 2016 and references therein).

Table 3

Adjusted repeatability estimates for the investigated traits across different time periods

	V_I	V_R	R
Overall			
Expl (PC) ^{abc}	0.88 (0.59; 1.26)	1.66 (1.30; 2.20)	0.34 (0.23; 0.47)
Time TR ^d	0.36 (0.18; 0.87)	0.60 (0.43; 0.91)	0.44 (0.24; 0.64)
Time NB ^{ab}	0.39 (0.18; 0.86)	0.51 (0.35; 0.77)	0.46 (0.26; 0.68)
Time FE	0.28 (0.13; 0.78)	0.75 (0.50; 1.06)	0.33 (0.15; 0.55)
Short term			
Expl (PC) ^c	0.58 (0.35; 0.94)	1.17 (0.84; 1.74)	0.33 (0.20; 0.49)
Across season			
Expl (PC) ^d	0.63 (0.17; 2.01)	1.78 (1.10; 3.04)	0.25 (0.09; 0.57)
Time TR ^d	0.35 (0.10; 0.94)	0.62 (0.36; 1.01)	0.41 (0.17; 0.66)
Time NB ^a	0.33 (0.10; 0.66)	0.50 (0.35; 0.92)	0.35 (0.15; 0.58)
Time FE	0.34 (0.12; 0.97)	0.76 (0.47; 1.20)	0.35 (0.13; 0.60)
Across year			
Expl (PC) ^b	0.71 (0.15; 1.55)	1.57 (0.91; 2.35)	0.30 (0.10; 0.55)
Time TR	0.36 (0.11; 0.86)	0.85 (0.49; 1.28)	0.31 (0.12; 0.56)
Time NB ^b	0.30 (0.13; 0.76)	0.47 (0.31; 0.81)	0.41 (0.20; 0.64)
Time FE	0.39 (0.08; 0.80)	1.01 (0.63; 1.54)	0.25 (0.09; 0.49)

For description of behavioural traits see Table 2. All models (both univariate and multivariate) included male ID as random intercept, and season and/or year as fixed effects. V_I is between-individual variance, V_R is within-individual (residual) variance and R is the adjusted repeatability. Results are presented as means with 95% credible intervals. Overall = all three repeated measurements, short term = within spring 2011, across season = across spring 2011 and autumn 2011 and across year = across spring 2011 and spring 2013.

^a Season was significant fixed effect.

^b Year was significant fixed effect.

^c Estimates from univariate mixed model presented (due to unbalanced experimental design).

Behavioural Repeatability

Exploration and sociability traits were moderately repeatable across seasons and years (range 0.25–0.41). Given that repeatability is generally thought to set an upper limit to heritability (Boake, 1989; but see Dochtermann, et al., 2015), our findings suggest that these traits have a genetic basis and hence the potential to evolve under selection, although this merits further study, implementing a quantitative genetic approach (e.g. Boake, 1989; Dingemanse & Dochtermann, 2014; Réale & Dingemanse, 2012). Interestingly, repeatability estimates did not decrease with increasing intertrial intervals (Bell et al., 2009), indicating that between-individual variation for these particular traits in this species was not affected by seasonal context and remained

consistent over substantial parts of the life span. So regardless of population level plasticity for some traits (see above), individual differences were maintained and stable.

The long-term maintenance of consistency is one of the key assumptions within theories linking personality and life history strategies (cf. POLS, Réale, Garant, et al., 2010; see also Wolf et al., 2007). In great tits, for example, consistent and heritable individual differences in exploration behaviour have been linked to survival and offspring recruitment (review in Dingemanse & Réale, 2005), and individuals have been shown to adjust their exploration behaviour in relation to their future survival prospects (Nicolaus et al., 2012). This suggests that life history trade-offs might be key in explaining the adaptive evolution of personality (see also Dammhahn, 2012; Hall et al., 2015; Niemelä, Vainikka, Hedrick, & Kortet, 2012). At present, little is known about exploration behaviour in starlings, but a few studies indicate that aspects of exploration in the laboratory are related to circulating hormone levels (Apfelbeck & Raess, 2008), learning performance (Boogert, Reader, & Laland, 2006), environmental sensitivity (Minderman et al., 2009) and home range size in the wild (Minderman et al., 2010), indicating its ecological relevance. Our findings are in line with recent empirical studies revealing long-term consistency in exploration behaviour (David et al., 2012; Hall et al., 2015; Koski, 2011; Wuerz & Krüger, 2015). Together, this suggests that exploration behaviour is an ecologically relevant, long-term stable personality trait in a variety of species that is shaped by selection and associated with differences in life history.

Similarly, long-term consistency in sociability is likely to be affected by selection and to influence life history trade-offs, especially in highly gregarious species (e.g. Farine & Sheldon, 2015; Formica et al., 2012; Koski, 2014; Oh & Badyaev, 2010). We found that male starlings differed consistently in their social tendency (Time FE), in line with findings in other studies (e.g. Aplin et al., 2015; Cote & Clobert, 2007; Cote et al., 2010; Koski, 2011). Differences in this tendency are known to be functionally significant, as they influence dispersal (Cote & Clobert, 2007; Cote et al., 2010), disease transmission (Hamede, Bashford, McCallum, & Jones, 2009), competition for breeding territories (Farine & Sheldon, 2015) and reproductive success (Formica et al., 2012; Oh & Badyaev, 2010; see Koski, 2011 for review of primate and human studies). Moreover, male starlings also differed consistently in the time they spent near the nestbox (Time NB). In spring, Time NB is assumed to reflect differences in the investment in mate attraction ('nestbox advertisement'), and hence is likely to influence the reproductive success

Table 4

Between- and within-individual correlation between the investigated traits across different time periods

	Expl (PC)	Time TR	Time NB	Time FE
Overall				
Expl (PC)	—	−0.31 (−0.64; 0.37)	−0.20 (−0.60; 0.43)	0.29 (−0.44; 0.65)
Time TR	0.20 (−0.08; 0.42)	—	0.57 (0.21; 0.85)	0.64 (0.18; 0.87)
Time NB	0.20 (−0.07; 0.44)	0.41 (0.20; 0.61)	—	0.14 (−0.49; 0.59)
Time FE	0.11 (−0.10; 0.41)	0.70 (0.55; 0.81)	−0.16 (−0.39; 0.10)	—
Across season				
Expl (PC)	—	0.10 (−0.70; 0.58)	−0.11 (−0.66; 0.53)	0.21 (−0.61; 0.68)
Time TR	0.02 (−0.29; 0.38)	—	0.54 (0.03; 0.87)	0.83 (0.33; 0.92)
Time NB	0.10 (−0.19; 0.42)	0.45 (0.16; 0.70)	—	0.14 (−0.46; 0.68)
Time FE	0.04 (−0.28; 0.40)	0.75 (0.52; 0.86)	−0.13 (−0.44; 0.21)	—
Across year				
Expl (PC)	—	−0.26 (−0.75; 0.45)	−0.12 (−0.72; 0.41)	0.17 (−0.61; 0.67)
Time TR	0.32 (−0.08; 0.54)	—	0.52 (−0.08; 0.55)	0.62 (0.09; 0.88)
Time NB	0.38 (−0.01; 0.58)	0.47 (0.16; 0.69)	—	−0.15 (−0.63; 0.52)
Time FE	0.15 (−0.14; 0.48)	0.81 (0.61; 0.87)	−0.13 (−0.37; 0.24)	—

For description of behavioural traits see Table 2. Exploration scores of the first two exploration trials were averaged before analyses. Each model, with all four behavioural traits as response, included male ID as random intercept, and season and/or year as fixed effects. Between-individual correlations (r_I) are presented above the diagonal and within-individual correlations (r_R) below the diagonal. Results are presented as means with 95% credible intervals. Significant correlations are highlighted in bold. Overall = all three repeated measurements, across season = across spring 2011 and autumn 2011 and across year = across spring 2011 and spring 2013.

of male starlings (Gwinner et al., 2002; Pinxten & Eens, 1990). The apparent influence of long-term consistency in social behaviours on a wide variety of ecologically relevant processes and ultimately fitness suggests that life history trade-offs favour their adaptive evolution (Réale, Garant, et al., 2010; Wolf et al., 2007).

Another possibility is that long-term consistency in (correlated) social behaviours evolved because it makes individuals predictable in certain types of social interactions (see Wolf, Van Doorn, & Weissing, 2011). Interestingly, we found that individual differences in the time spent near the nestbox were maintained across seasons, even though this is assumed to reflect functionally different behaviours in different seasons (e.g. Eens et al., 1990; Pinxten, De Ridder, De Cock, et al., 2003). One might therefore argue that mate attraction behaviour in the breeding season and competition behaviour outside the breeding season represent a behavioural syndrome (sensu Stamps & Groothuis, 2010). Such a suite of social behaviours might have resulted from correlational selection, hence making an individual's social behaviour predictable across social contexts (i.e. mating and competition; Sinervo & Svensson, 2002; Wolf, Doorn, & Weissing, 2011). Variation in both traits is also likely to relate to social dominance, affecting competition for resources (e.g. nest location or roosting place; see Feare, Gill, McKay, & Bishop, 1995; Gwinner et al., 2002; Witter & Swaddle, 1995). This might have important implications for access to potential mates and social organization within more complex social environments (e.g. McGhee & Travis, 2010; Oh & Badyaev, 2010; Pike, Samanta, Lindstrom, & Royle, 2008; Wolf & Krause, 2014). One interesting step forward would therefore be to investigate how the observed long-term consistent individual differences in mate attraction behaviour, competition and possibly dominance interact in determining fitness and life history trade-offs within flocks.

Between- and Within-individual Correlations

Despite their moderate repeatability across seasons and years, exploration behaviour and sociability traits did not covary between individuals. The absence of significant correlations might be due to a lack of power associated with our modest sample size and number of repeated measurements per individual (see Dingemanse & Dochtermann, 2013). Our results should therefore be interpreted with some caution and future studies should aim to obtain larger sample sizes. Bearing this in mind, our findings suggest that exploration behaviour and the sociability traits investigated do not constitute behavioural syndromes in our population of male starlings. Since there is substantial evidence that phenotypic correlations are generally informative about the sign and magnitude of underlying genetic correlations and hence evolutionary implications (see Dochtermann, 2011; Dochtermann & Dingemanse, 2013), our results suggest that the investigated traits might have the potential to evolve independently from each other (Roff & Fairbairn, 2007), which merits further investigation.

The few studies investigating behavioural syndromes between sociability and other personality traits have provided mixed results, with some studies finding no relationship (Haage et al., 2013; McEvoy et al., 2015; our study) and others reporting positive associations (Badyaev, 1997; McCowan et al., 2015). There are at least two potential reasons for this apparent discrepancy. First, from an evolutionary perspective, if behavioural syndromes arise as a result of adaptive evolution in response to local selection pressures, they might not be present in all species, or populations of the same species (see e.g. Dingemanse et al., 2007; Garamszegi, Markó, & Herczeg, 2012; Garamszegi et al., 2015). Second, from a developmental perspective, if behavioural syndrome structures are not stable across ontogeny or age, they might arise or disappear even within the same (group of) individuals (see e.g. Class & Brommer, 2015; Stamps & Groothuis,

2010; Wuerz & Krüger, 2015). Together, this emphasizes the need for long-term studies investigating different aspects of sociability and their relationships with other personality traits in wild populations experiencing different selective environments (e.g. Class & Brommer, 2015; Garamszegi et al., 2015; Stamps & Groothuis, 2010).

Furthermore, we found that different sociability traits (i.e. Time FE and Time NB) did not covary between individuals, indicating they represent independent aspects of male starlings' social personality. Hence, regardless of the above-described potential behavioural syndrome integrating mate attraction and competition (and possibly dominance), social tendency might not be part of this suite of social behaviours. Studies directly addressing relationships between different social personality traits are scarce (see Koski, 2011 for primate and human studies). One recent study in the common waxbill, *Estrilda astrild*, found that social dominance was due to body size rather than social tendency or other personality traits (Fungghi, Leitão, Ferreira, Mota, & Cardoso, 2015). This indicates that social tendency might not relate to competition and dominance, in line with our findings. It is worth noting here that significant between-individual (as well as within-individual) correlations between Time FE and Time NB on the one hand, and the total time spent responding (Time TR) on the other, are simply the result of the way Time TR is calculated and hence do not represent any biologically meaningful correlations.

Interestingly, exploration and time spent near the nestbox tended to positively covary within individuals (while none of the other traits did) across breeding seasons (spring 2011 and spring 2013). Within-individual correlations arise when two (or more) traits change in concert in response to a common environmental (e.g. temperature, predation pressure) and/or internal factor (e.g. hormones; Dingemanse & Dochtermann, 2013). This suggests that when a given individual was more exploratory during an exploration trial it had a higher chance of detecting the nest hole and therefore was more likely to spend time there during the subsequent sociability trial. Although this seems plausible, as by definition, exploration behaviour provides individuals with information about their environment (Renner, 1990), this explanation is not supported by our observations. Indeed, birds were never observed to hang in the nest hole or enter the nestbox during any of the exploration trials. However, we cannot exclude the possibility that individual males differed in other aspects of exploration, such as scanning (see Renner, 1990), potentially causing individual differences in the chance of detecting the nest hole. Nevertheless, our observations indicate that behaviours directed towards the nest hole were solely triggered by the presence of the female, validating Time NB as a measure of social behaviour in starlings (cf. Eens et al., 1990; Eens et al., 1993; Gwinner et al., 2002). Another possibility is that proximate mechanisms such as circulating hormone levels (e.g. testosterone, corticosterone) simultaneously affect the expression of exploration behaviour and nestbox advertisement within individuals, but this largely remains to be tested (but see Apfelbeck & Raess, 2008; Mutzel et al., 2011; Pinxten et al., 2003).

In conclusion, our study provides empirical evidence that exploration behaviour and different sociability traits are repeatable across seasons and in the long term, but do not form behavioural syndromes. Given recent evidence that most personality traits are heritable (Dochtermann et al., 2015), this suggests that exploration and sociability traits have the potential to evolve independently in response to selection. However, to adequately understand the ecological and evolutionary significance of these consistent differences, our findings await cross-validation with results from the wild (see Niemelä & Dingemanse, 2014). Subsequently, research into their relation with other behaviours in complex social environments and ultimately fitness will provide insights into how selection might act in maintaining these personality differences.

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