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Heritability and social brood effects on personality in juvenile and adult life-history stages in a wild passerine

Running title: Heritability of personality

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Abstract

How has evolution led to the variation in behavioural phenotypes (personalities) in a population? Knowledge of whether personality is heritable, and to what degree it is influenced by the social environment, is crucial to understanding its evolutionary significance, yet few estimates are available from natural populations. We tracked three behavioural traits during different life-history stages in a pedigreed population of wild house sparrows. Using a quantitative genetic approach, we demonstrated heritability in adult exploration, and in nestling activity after accounting for fixed effects, but not in adult boldness. We did not detect maternal effects on any traits, but we did detect a social brood effect on nestling activity. Boldness, exploration and nestling activity in this population did not form a behavioural syndrome, suggesting that selection could act independently on these behavioural traits in this species, although we found no consistent support for phenotypic selection on these traits. Our work shows that repeatable behaviours can vary in their heritability, and that social context influences personality traits. Future efforts could separate whether personality traits differ in heritability because they have served specific functional roles in the evolution of the phenotype, or because our concept of personality and the stability of behaviour needs to be revised.

Keywords: quantitative genetics, repeatability, additive genetic variation, house sparrows, animal model.

Introduction

Individuals often behave consistently through time and/or contexts but differently from conspecifics (Wilson, 1998; Sih *et al.*, 2004a; b; Réale *et al.*, 2007). Such repeatable behaviours, called personality, imply a degree of behavioural inflexibility when individuals respond to environmental variation. Theory suggests that such personalities could be adaptive (Dall *et al.*, 2004; Dingemanse & Wolf, 2010). Empirical results suggest that artificial and natural selection can act on personality over short timescales (Dingemanse *et al.*, 2004; van Oers *et al.*, 2004). Nonetheless, personality can only evolve in response to selection if between-individual differences and/or within-individual variation in behaviour are heritable. The evolutionary potential of any trait must also be viewed in the context of parental effects, social interactions, indirect genetic effects, experience, age and other personality traits. These factors have independent effects on evolutionary potential and can bias estimates of heritability and, subsequently, evolutionary potential of personality (Wolf *et al.*, 1998; Qvarnström & Price, 2001; Bijma, 2014). Relatively few studies in wild populations have focused on the heritability of traits with large environmental influences (Hadfield *et al.*, 2007), or on personality in particular (Oers & Sinn, 2013; Dochtermann *et al.*, 2014). One point to consider with such variable traits is whether the residual (within-individual) variance has a biologically meaningful origin, such as intra-individual variation or plasticity (Stamps *et al.*, 2012; Westneat *et al.*, 2015), or whether this variance is mainly composed of measurement error. Considering the heritability of between-individual differences minus within-individual variation (*sensu* Dochtermann *et al.*, 2014) could lead to heritability estimates that better predict the response to selection. Thus by appreciating within-individual variance, our impression of the evolutionary potential of variable traits, including personality, can be improved.

Heritability can be obscured or inflated by environmental sources of similarity between relatives, such as maternal effects and social effects. Maternal effects are influences of the mother on the phenotype of the offspring (Qvarnström & Price, 2001), through, for example, nutrition, hormone deposition in gametes, and epigenetics, and can change the phenotype and fitness of an offspring (Champagne *et al.*, 2003; Schroeder *et al.*, 2012). To estimate heritability accurately, it is essential to account for maternal effects whenever they increase the similarity between relatives beyond genetic similarity (Kruuk & Hadfield, 2007; Noble *et al.*, 2014). Despite this, maternal effects have not always been accounted for in animal personality studies (Taylor *et al.*, 2012), possibly because separating maternal and direct genetic effects requires manipulations such as cross-fostering, and/or large sample sizes when using pedigree-based approaches (Kruuk & Hadfield, 2007). Individuals can become more similar through feedback from a shared social environment. For example, the number and sex of siblings can determine the nature of within-family competition, and such competition may affect behaviour and fitness (Nicolaus *et al.*, 2009; Hadfield *et al.*, 2013). Crucially, social interactions can mask the repeatability and heritability of a behaviour, because such social interactions can enhance differences between individuals or, alternatively, homogenise behavioural responses within groups (Wilson, 2014). Quantifying maternal effects and social brood effects is essential for understanding the formation of personality traits, and therefore how personality traits could respond to selection.

Lastly, personality traits may be correlated with each other, forming a behavioural syndrome (Bell *et al.*, 2009; Dingemanse *et al.*, 2010). Behaviours could become functionally linked as a result of predation or plasticity, or from a shared genetic or developmental basis. Genetically linked traits can facilitate or constrain evolutionary potential because such traits cannot evolve completely independently from one another (Dochtermann & Dingemanse, 2013). Frequently, studies measure correlations between behaviours within a life-history stage (e.g., Brommer & Kluen, 2012). However, selection pressures may change across life-history stages, leading to changes in personality (Groothuis & Trillmich, 2011). Personality has been tracked across life-history stages in insects (Hedrick & Kortet, 2011), mammals (Gracceva *et al.*, 2011; Petelle *et al.*, 2013), and birds (Carere *et al.*, 2005; Naguib *et al.*, 2011; McCowan & Griffith, 2014; Favati *et al.*, 2016). However, most of these studies have been done in captivity, potentially because it is difficult to phenotype and genotype a population of wild individuals repeatedly throughout their life-history, especially at young ages (Oers & Sinn, 2013). The few existing studies across life-history stages in wild birds show that the same behavioural measures can be positively, negatively, or not correlated across contexts (Kluen & Brommer, 2013;

Class & Brommer, 2015; Garamszegi *et al.*, 2015; Edwards *et al.*, 2017). Therefore, we do not know whether our measures of behavioural syndromes in captivity and within a life-history stage reflect what happens in the wild and across life-history stages. In particular, heritability estimates are lacking from wild populations for individuals measured as both juveniles and adults.

Here, we study three behavioural traits, boldness, exploration and nestling activity, in wild house sparrows, *Passer domesticus*. We used an exceptionally comprehensive behavioural and genetic data set to address three hypotheses. 1) The behavioural traits we measured are repeatable or stable within individuals, and are therefore personality traits. 2) The repeatable portion of these behavioural traits stems from additive genetic, maternal and social effects that explain between-individual differences in personality. 3) A behavioural syndrome exists between the behavioural traits across life-history stages, based on the presence of correlations between these traits within life-history stages in other species (Garamszegi *et al.*, 2013). We also calculated phenotypic selection gradients for the adult traits to provide context for the heritability of these traits. This is one of few studies to track the heritability of personality in wild individuals as both juveniles and adults (Petelle *et al.*, 2013, 2015; Class & Brommer, 2015; Patterson *et al.*, 2015, though see references therein for wild-caught individuals tested in the lab) and to test whether personality has the genetic basis necessary to evolve.

Methods

Population

Behavioural and genetic data were collected from the Lundy Island house sparrow population, Lundy Island, UK, where breeding and survival have been comprehensively monitored since 2000 (Nakagawa *et al.*, 2007; Schroeder *et al.*, 2011). This population has extremely low rates of immigration and emigration, and high resighting probabilities (Simons *et al.*, 2015), so the survey has very limited bias. A large proportion of nestlings were cross-fostered on the day after hatching

(Winney *et al.*, 2015). This manipulation increases our power to separate pre-manipulation maternal effects from additive genetic and post-manipulation environmental (social brood) effects (Kruuk & Hadfield, 2007).

Boldness

Boldness data were collected during the breeding seasons in 2009 (pilot year) and 2011–2014. We measured breeding adults' reactions to a white piece of paper (width 3.4 cm) that was taped to the inside of the nest box entrance such that it covered the entrance hole (Figure S1a, similar to Garamszegi et al. 2009) when the brood was 9 days old (hatching=day 1). Breeding pairs were presented with the novel object for 60 minutes, and their reactions were video recorded. Pairs had already habituated to the cameras during routine monitoring (Nakagawa *et al.*, 2007). From these videos, we scored male and female latency (in decimalised minutes) from touching to entering the nest box. Focal individuals were tested between one and four times annually, once for each brood. Boldness observations of bigamous males were excluded (Text S1).

Social parents were identified from colour-ring sightings, transponder readings, and captures (Nakagawa *et al.*, 2007; Schroeder *et al.*, 2011). For the 2011 to 2013 broods, parents that could not be identified in the field were assigned as social mothers if they were the genetic parent of all offspring, or social fathers if a male was the genetic father of a majority of the offspring in the brood, and their colour-rings matched the available sighting information. We assigned 26 males and 26 females with this method for 2011–13, and were lacking pedigree data to do this for 2014.

Exploration

We collected exploration data from 2010–2014 in two sampling events that took place each year between November and March (non-breeding season), one week in October-December and one week in January-March. Birds were caught, measured, and DNA sampled. Birds were then rested in a bird bag before being released into a novel environment (rest time measured to the nearest five minutes: median 20 min, SD 18.5 min, range 0–100 min). The novel environment was a domed tent containing two artificial bamboo-cane trees (Figure S1b, described in Sánchez-Tójar et al. 2017) . Birds were observed for five minutes through a mesh triangle (approximately 5x5x7 cm). The tent was backlit with a halogen lamp (model GT2Q-L500) so that the observer's shadow was projected away from the tent. The hidden observer counted the number of flying and running movements made by the focal bird. A run consisted of ground-based hopping covering half the length of a tent side (1.37 metres, approximated by the observer), excluding cases where a bird doubled back on itself. A flight was either a movement within and between tree branches and stands, or a take-off, flapping and stable landing.

Nestling activity

Nestling activity data were collected during breeding between April and August in the years 2011–2013. In 2011, we assessed nestlings once per day on days 10, 12 and 13, but we stopped testing on day 13 because some nestlings were able to fly. To calculate repeatability over two days, rather than three, we increased the number of tests to three times per day on each of days 10 and 12. Our analyses are based on all data to maximise power. Nestlings were placed in a circular arena marked with a grid pattern and surrounded by a wall (Figure S1c, described in Sánchez-Tójar et al. 2017). We video-recorded the nestlings' activity and recorded the total number of squares a nestling crossed in 30 seconds. Nestlings that did not move were given a score of one. Additional details are available in Text S1. One observer watched all videos in order. We confirmed that the observations were repeatable between observers and confirmation bias was negligible (Text S1).

Genetic pedigree

We used a genetic pedigree to estimate the additive genetic variance component of each trait (Hsu *et al.*, 2014; Schroeder *et al.*, 2015). Following Taylor *et al.* (2012), we assigned unique artificial maternal identities to all birds that did not have a genetic mother assigned (11 observations of seven individuals for boldness, six observations of four individuals for exploration). This allowed us to use all available phenotypic information, but assumed that these birds are independent data points for calculating a maternal effect. This includes three birds that were phenotyped but not yet genotyped. We used the package *pedantics* to present summary statistics (Morrissey & Wilson, 2010) in R version 3.3.2 (R Development Core Team, 2013). We used the inverse relationship matrix of this pedigree for animal models in *ASReml-R* 3 (Butler, 2009). Summary statistics for the full pedigree and the informative pedigree for each trait are listed in Table S1. Additional details on our pedigree are available in Text S1, and a power analysis for the pedigree with filled-in missing dams is detailed in Text S2.

Annual fitness

Annual fitness was approximated as the number of offspring in the pedigree assigned to a given sire or dam within a year. Our pedigree includes unhatched eggs and nestlings from two days old, thus this measure of fitness does not include the fitness of the offspring. We correlated boldness with the number of offspring in the same year, and exploration with number of offspring in the following summer. Adult exploration was correlated to annual fitness in the following summer to address the question of whether behaviour influences fitness.

Statistical analysis

We log-transformed all behavioural traits (adding 0.5 to boldness and exploration that had a minimum score of zero, and subtracting 0.5 from activity that had a minimum score of one) to approximate normality (Text S1). . Log-transformed latency to enter the nest box was multiplied by -1 so that larger values implied an individual was becoming bolder and *vice versa*. Occasionally, our tests were disturbed by island residents or test-specific events and we recorded when this happened. As we were uncertain whether these boldness tests were compromised by such disturbances, leading to unusual behaviour by the focal pair (146 compromised, seven taken on an incorrect day, details in Text S1), we excluded these boldness measures (Text S1).

We estimated the repeatabilities (intra-class correlation coefficient, ICC, Nakagawa & Schielzeth, 2010) for the behavioural traits within years or life-history stages of the birds, across these categories and overall. Then we estimated the additive genetic, maternal and permanent environment variance components for each trait. Lastly, we estimated covariances amongst these behavioural traits and between the adult behavioural traits and a measure of annual fitness. We used Linear Mixed effects Models (LMMs) in the software *ASReml-R* (Butler, 2009) to calculate repeatabilities and heritabilities.

Repeatabilities, heritabilities and proportions of variance were calculated by dividing the variance component(s) of interest by the sum of all variance components. In calculating repeatabilities in this way, we are assuming that between-individual variance attributable to grouping factors, such as mothers, has a negligible effect on within- and between-individual variance in the repeatability models, and that the findings on the data after applying transformations for normality approximate the findings on the original data scale (Nakagawa & Schielzeth, 2010). Standard errors were calculated by Taylor series approximation with function pin() based on the delta method (Oehlert, 1992). We checked the model fits by plotting model residuals.

Repeatability

Personality is the repeatable component of behaviour, and strongly consistent traits have repeatabilities closer to one. We assessed how consistent each behaviour was by calculating repeatabilities, or intra-class correlation coefficients. Repeatability is the ratio of variance explained by between-group differences over the sum of between-group and within-group variances (Lessells & Boag, 1987; Sokal & Rohlf, 1995; Nakagawa & Schielzeth, 2010). We used LMMs to calculate repeatabilities because this method can incorporate environmental variables, allow for nested group factors, and estimate variances directly. Hence, we calculated repeatabilities as the variation among individuals (V_{ind}) divided by all variation in the data (V_{R}, Nakagawa & Schielzeth 2010). We considered repeatabilities <0.3 as low, and <0.5 as medium, using the average repeatabilities of Bell et al. (2009) as our baseline. We first calculated the repeatability of boldness, exploration and nestling activity across all tests by running an intercept-only LMM of the transformed trait with bird identity (ID) as the only random effect. Next, we explored whether repeatability varied between different groups or timeframe. A significant difference between two repeatabilities is approximated by doubling the standard errors for the two groups, and if the limits of the double standard errors do not overlap, the two repeatabilities are considered significantly different (i.e. the possible estimates for the two variance components are non-overlapping). For the adult traits, we asked if there was sex-specific repeatability. Then we calculated the within-summer (breeding, April to September) repeatability for boldness and within-winter (non-breeding, October to March) repeatability for exploration by restricting our data set. For nestling activity, we calculated the individual repeatability within days 10 and 12. Lastly, for all traits, we calculated the repeatability across summers, winters or days by taking the first measure of an individual within each timeframe.

Boldness was measured on two individuals (both parents attending the brood in the nest box) at the same time and was initially analysed as two co-varying traits to gain insight into the feedback that might occur between males and females. However, just eight females and ten males were measured with more than one partner and the models did not converge, so we only present the univariate models.

Heritability

To estimate the heritability of personality, we incorporated a pedigree into the LMMs to quantify the additive genetic variance component to each trait (animal model, Falconer and McKay 1996). For these quantitative genetic models, we included maternal ID, bird ID and pedigree-linked bird ID terms as random effects to quantify maternal (V_M), permanent environment (V_{PE}), and additive genetic (V_A) effects, respectively on boldness, exploration and nestling activity. Our cross-fostering manipulation separated pre-manipulation (maternal) effects from post-manipulation (social brood and rearing environment) effects, which increased our power to separate additive genetic from maternal effects on boldness and exploration. Within the nestling activity data, multiple individuals were measured from each brood. Therefore, the nestling activity model included a social brood ID (V_S) term to separate maternal from rearing environment effects. It was not possible to fit a brood ID term to the adult trait models because too few brood-mates survived. The models presented in the main text are run without fixed effects so that the resulting repeatabilities and heritabilities are independent of these fixed effects and can be compared within this study and between studies (Wilson, 2008). Results including fixed effects are in Text S3.

Heritabilities can be calculated in two ways. The total variance ($V_{PE} + V_M + V_A + V_S + V_R$) describes the variation within the measured behaviour. Removing the residual variance from this leads to a description of the variance between individuals ($V_{PE} + V_M + V_A + V_S$). The residual variance is a measure of within-individual variability, which includes measurement error and individual plastic responses. Thus, removing the residual variance focuses a calculation on between-individual differences. Residual variance can indicate intra-individual variability that could be repeatable in its own right, and can reflect plasticity to an unmeasured variable (Stamps *et al.*, 2012; Westneat *et al.*, 2015).

Therefore, heritability of behaviour is the additive genetic variance divided by the total variance, whilst the heritability of personality can be viewed as the additive genetic variance divided by the variance between individuals (Dochtermann *et al.*, 2014).

Behavioural syndrome

We estimated the covariances between the three personality traits in a trivariate model. We fitted boldness, exploration and nestling activity as dependant variables and allowed them to covary between individuals. We *z*-transformed the variables (subtracted the mean and divided by one standard deviation) so that all covariances were comparisons between similarly scaled traits. The three behavioural traits were measured at different times and did not temporally overlap, therefore we restricted the within-individual (residual) covariation to zero. The initial between-individual covariance matrix was unconstrained, and we tested the significance of each covariance by fixing the focal covariance to zero and comparing twice the difference in log-likelihood between this model and the unconstrained model. We used a χ^2 distribution with one degree of freedom to test for significance of covariances. However, the true χ^2 distribution would have 0.5 degrees of freedom (Self & Liang, 1987), so these χ^2 values are highly conservative.

Selection gradients

Lastly, we calculated selection gradients for the adult traits for each year and for each sex, separately, so that the same offspring was not assigned as a unit of fitness twice in the same analysis. We took first the mean measure of the trait per individual per year to have a single measure per individual, and logged, scaled, and centred the traits. Pearson's product moment correlations between the behavioural trait and annual fitness within a year were calculated and are presented as phenotypic selection gradients.

Selection was calculated for boldness in 2011-13 and exploration in 2012-13 because in these years we had pedigree information and the largest sample sizes to calculate these correlations.

Results

Data summary

We video recorded 279 broods and tested 184 adult sparrows between one and nine times each for boldness, with 90 individuals tested more than once. The median entry latency was 3.6 minutes (standard deviation SD 9.23, range: 0.0 to 46.8 min, Figure 1) and the distribution was right-skewed.

For exploration, we used data from 450 tests on 282 individuals, 117 of which were tested between two and six times. The median number of movements was eight (SD 21.9, range: 0–169) and the distribution was right-skewed with some zero-inflation (Figure 1).

Five hundred and fifteen nestlings were tested for activity in 2,853 tests from 2011 to 2013 (median: 6 squares, SD 8.72, range: 1–84, Figure 1). On day 12, more nestlings have higher activity and more nestlings have a score of one than on day 10, leading to a wider distribution (Figure 1). The distribution was also quite stochastic on day 12 at low values: in 234 tests nestlings scored one, 60 scored two and 103 scored three. This stochasticity could arise from nestlings travelling a minimum distance to go from the centre of the arena to the arena wall, and a small number of additional values of one will result from a nestling reaching the edge of the arena before assessment of the nestling's behaviour began (when the releaser's hand was removed). The analysis focuses on the variance in nestling activity and not on the fixed effects explaining nestling activity; therefore we believe the analysis of this trait is relatively unbiased.

Repeatability

Boldness had low repeatability across all tests within each sex (all tests 0.18 ± 0.07 SE, males 0.15 ± 0.10, females 0.21 ± 0.09, Table 1). The repeatability from the first test per year was not statistically significantly different from zero (0.14 ± 0.13, Table 1).

Repeatability of exploration was moderate across all data points and within winters (all traits 0.29 ± 0.07, Table 1). Females and males did not differ significantly (females 0.42 ± 0.09, males 0.20 ± 0.09, Table 1).

The repeatability of nestling activity across all tests and across days was modest, and was highest for day 12 nestlings (all tests: 0.25 ± 0.02, day 10: 0.36 ± 0.03, day 12: 0.47 ± 0.03, Table 1).

Heritability

There was no significant additive genetic variation and no maternal effect on boldness in an intercept-only model (Table 2, Figure 2). Any maternal effect in this study stem from genetic and early environmental effects, since cross-fostering separates the majority of these from later maternal effects (26% of adults measured for boldness, 39% of adults measured for exploration, and 59% of nestlings for nestling activity were cross-fostered). The heritability of the behaviour and thus of personality was also not significant (0.04 ± 0.07 and 0.21 ± 0.37, respectively, Table 2, Figure 2). However, our power to detect heritability was lowest for boldness (Text S2). Nearly all individual consistency was attributable to permanent environment effects (0.15 ± 0.09 for the behaviour and 0.79 ± 0.37 for personality, Table 2, Figure 2).

There was significant additive genetic variation in exploration behaviour (0.26 ± 0.07), such that a large proportion of the repeatability of exploration behaviour was attributed to additive genetic effects (0.80 ± 0.14, Table 2, Figure 2). Our power to detect significant additive genetic variance of 0.26 was good, especially for a personality study in a wild population: 0.48 when maternal effect variance was 0.3 and 0.71 when maternal effect variance was 0 (Figure S3), though as with any estimate of additive genetic variance this should be seen as an estimate rather than an exact value. Permanent environment effects could not be estimated, and maternal effects were small (0.07 ± 0.05, Table 2, Figure 2), indicating that more variance in exploration is attributable to additive genetic than other effects.

There was no significant additive genetic variation in nestling activity when excluding fixed effects (as a behavioural or a personality trait) across all tests and within days 10 and 12 (Table 2, Figure 2), though there was after accounting for fixed effects (0.08 ± 0.04, Table S4). There were no maternal effects from genetic or early environment sources, which contrasted with the effects of the social brood (Table 2, Figure 2). Social brood effects were a similar magnitude to additive genetic effects, though were statistically significant, on day 10 (0.07 ± 0.03) and across all days (0.09 ± 0.02), and became greater on day 12 (0.17 ± 0.04, Table 2, Figure 2). These statistically significant social brood effects indicate that social brood members behave similarly and that there is variance between broods in mean behaviour. Social brood effects persisted after accounting for sources of similarity such as brood size, nestling mass or test conditions (Text S3, Table S4). A large proportion of behaviour and personality at each age was attributed to permanent environment effects of unknown source (Table 2, Figure 2).

Table 1: Intercept-only repeatabilities (intra-class correlation coefficients, ICCs) and sample sizes for boldness, exploration and nestling activity in Lundy Island house sparrows, with standard errors. ICCs are calculated by dividing the variance attributable to individual consistency (V_{ind}), by the total variance including residual variance (V_{R}). Boldness, exploration and activity were log-transformed after adding 0.5 to boldness and exploration and subtracting 0.5 from activity. P-values for random effects were calculated with likelihood-ratio tests. χ^2 tests were conducted with one degree of freedom. 'Boundary' denotes terms that could not be estimated by the model and are given a very small value on the edge of parameter space.

	N_{ind}	$N_{\text{[ind with repeats]}}$	N_{obs}	Intercept ± se	V_{ind} ± se	V_{R} ± se	ICC ± se	χ^2
Boldness								
All tests	184	90	387	-1.51 ± 0.07	0.23 ± 0.09	1.00 ± 0.09	0.18 ± 0.07	8.94, p=0.003
Male	80	33	151	-1.60 ± 0.11	0.21 ± 0.15	1.15 ± 0.17	0.15 ± 0.10	3.09, p=0.079
Female	104	57	236	-1.45 ± 0.08	0.25 ± 0.11	0.90 ± 0.11	0.21 ± 0.09	6.05, p=0.014
Within year – 2009	4	0	4	-	-	-	-	-
Within year – 2011	64	17	81	-1.11 ± 0.12	0.04 ± 0.29	1.03 ± 0.33	0.03 ± 0.27	0.01, p=0.911
Within year – 2012	50	19	73	-1.33 ± 0.13	Boundary	1.25 ± 0.21	-	0.00, p=1.000
Within year – 2013	73	36	117	-1.69 ± 0.11	0.36 ± 0.19	0.84 ± 0.18	0.30 ± 0.14	3.22, p=0.073
Within year – 2014	76	30	112	-1.69 ± 0.11	0.28 ± 0.20	0.96 ± 0.21	0.23 ± 0.16	2.00, p=0.158
Across year (first measure only)	158	43	211	-1.62 ± 0.08	0.16 ± 0.16	1.01 ± 0.18	0.14 ± 0.13	0.97, p=0.325
Exploration								
All tests	282	117	450	2.11 ± 0.07	0.48 ± 0.12	1.17 ± 0.12	0.29 ± 0.07	22.0, p<0.001

Male	158	66	256	2.24 ± 0.09	0.34 ± 0.17	1.41 ± 0.18	0.20 ± 0.09	5.93, *p*=0.015
Female	124	51	194	1.94 ± 0.10	0.61 ± 0.17	0.85 ± 0.13	0.42 ± 0.09	21.1, *p*<0.001
Within winter – 2009	15	1	16	-	-	-	-	-
Within winter – 2010	20	1	21	-	-	-	-	-
Within winter – 2011	85	25	116	1.95 ± 0.13	0.24 ± 0.35	1.63 ± 0.38	0.13 ± 0.18	0.38, *p*=0.535
Within winter – 2012	99	33	142	2.26 ± 0.11	0.39 ± 0.21	1.18 ± 0.22	0.25 ± 0.12	5.00, *p*=0.025
Within winter – 2013	127	24	155	2.04 ± 0.11	0.72 ± 0.24	0.80 ± 0.20	0.47 ± 0.13	9.97, *p*=0.002
Across years (first measure only)	282	55	346	2.09 ± 0.07	0.49 ± 0.17	1.06 ± 0.17	0.32 ± 0.10	9.38, *p*=0.002
Nestling activity								
All tests	515	510	2853	1.58 ± 0.03	0.27 ± 0.03	0.82 ± 0.02	0.25 ± 0.02	287.1, *p*<0.001
Day 10	504	468	1438	1.65 ± 0.03	0.20 ± 0.02	0.34 ± 0.02	0.36 ± 0.03	160.5, *p*<0.001
Day 12	490	455	1398	1.53 ± 0.05	0.76 ± 0.07	0.87 ± 0.04	0.47 ± 0.03	275.6, *p*<0.001
Day 13	17	0	17	-	-	-	-	-
Across days (first measure only)	515	479	1010	1.74 ± 0.04	0.20 ± 0.05	0.91 ± 0.06	0.18 ± 0.04	18.8, *p*<0.001

Table 2: Variation between Lundy Island house sparrows in boldness, exploration and nestling activity, attributable to permanent environment (V_{PE}), additive genetic (V_A), maternal (V_M), social brood effects (V_S) and residual variance (V_R), with standard errors. The proportions of variance explained by each random effect are given under *pe*, h^2, *m* and *s* for permanent environment, heritability, maternal effects and social brood effects, respectively. The top proportion in each row is the proportion of all variance explained (i.e. of behaviour) and the bottom proportion in each row is the proportion of repeatable variance explained (i.e. of personality, Dochtermann *et al.*, 2014). The statistical significance of a variance component was calculated with a likelihood ratio test. Boldness, exploration and activity were log-transformed before entering the model. Sample sizes are given in Table 1. Boundary terms are variance components that cannot be estimated by the model. For heritability estimates including fixed effects, see Text S3.

	V_{PE}	χ^2	V_A	χ^2	V_M	χ^2	V_S	χ^2	V_R	*pe*	h^2	*m*	*s*
Boldness	0.19 ± 0.11	2.66, $p=0.10$	0.05 ± 0.09	0.36, $p=0.55$	Boundary	0.00, $p=1.00$	-	-	1.00 ± 0.09	0.15 ± 0.09	0.04 ± 0.07	-	-
										0.79 ± 0.37	0.21 ± 0.37	-	-
Exploration	Boundary	0.00, $p=1.00$	0.44 ± 0.14	14.3, $p<0.001$	0.11 ± 0.08	3.18, $p=0.07$	-	-	1.12 ± 0.10	-	0.26 ± 0.07	0.07 ± 0.05	-
										-	0.80 ± 0.14	0.20 ± 0.14	-
Nestling activity	0.13 ± 0.03	13.2, $p<0.001$	0.05 ± 0.03	1.98, $p=0.16$	Boundary	0.00, $p=1.00$	0.09 ± 0.03	20.7, $p<0.001$	0.82 ± 0.02	0.12 ± 0.03	0.05 ± 0.03	-	0.09 ± 0.02
										0.47 ± 0.11	0.19 ± 0.12	-	0.34 ± 0.08

Day 10	0.11 ± 0.03	14.0, $p<0.001$	0.05 ± 0.03	3.11, $p=0.08$	0.00 ± 0.01	0.01, $p=0.91$	0.04 ± 0.02	4.29, $p=0.04$	0.34 ± 0.02	0.20 ± 0.05	0.09 ± 0.06	0.00 ± 0.03	0.07 ± 0.03
										0.55 ± 0.14	0.25 ± 0.16	0.01 ± 0.07	0.19 ± 0.09
Day 12	0.38 ± 0.08	20.7, $p<0.001$	0.10 ± 0.08	2.19, $p=0.14$	Boundary	0.00, $p=1.00$	0.28 ± 0.07	29.1, $p<0.001$	0.87 ± 0.04	0.23 ± 0.05	0.06 ± 0.05	-	0.17 ± 0.04
										0.50 ± 0.10	0.14 ± 0.10	-	0.36 ± 0.08

Behavioural syndrome

We found no statistically significant between-individual correlations between traits (off-diagonal elements Table 3, Figure 3). In addition, the covariances between all traits were extremely small (-0.06 – 0.02, Table 3), such that these traits can be considered truly independent.

Selection gradients

There was no evidence for selection on either of the adult behavioural traits (Figure 4, Table S5).

Table 3: Correlations between z-transformed (scaled to one standard deviation and mean centred) boldness, exploration and nestling activity of Lundy Island house sparrows from a model of all three traits. Between-individual variances (± one standard error) are on the diagonals, between-individual covariances and chi-squared values (χ^2, the degree of freedom is 0.5 for covariances) are below the diagonals (dark grey) and phenotypic correlations, calculated from these variances and covariances, and sample sizes (*N*) above the diagonals (light grey). Residual variance is given on the right. Covariance significance is calculated with a likelihood ratio test comparing the log likelihood of the original model to a model where the focal covariance was fixed at zero. We included no fixed effects and did not estimate residual covariance. Boldness, exploration and activity were log-transformed. Diagonals here can be interpreted as raw correlations of a repeatedly measured individuals corrected for covariance with other traits.

	Boldness	Exploration	Activity	Resid. variance
Boldness	0.19 ± 0.07	-0.00 ± 0.02 *N*=101	-0.01 ± 0.01 *N*=52	0.82 ± 0.08
Exploration	-0.01 ± 0.07 χ^2=0.01	0.29 ± 0.07	0.01 ± 0.01 *N*=116	0.70 ± 0.07
Activity	-0.06 ± 0.07 χ^2=1.04	0.03 ± 0.05 χ^2=0.20	0.25 ± 0.02	0.75 ± 0.02

Discussion

The frequently untested premise of personality research is that personality traits have a genetic basis. Here, we found that the heritability of three traits in a wild pedigreed population ranged from high (adult exploration) to low or indistinguishable from zero (nestling activity and adult boldness, respectively, though our power to detect additive genetic effects was low for boldness, Text S2). Maternal effects were low but social brood (nestling activity) and partner effects (adult boldness) were high. The behavioural traits that we measured were not part of a behavioural syndrome across life-history stages, nor did we detect phenotypic selection on the adult behavioural traits. These results have implications both for how we carry out personality research and what we interpret from it. Therefore, we could question three things: when is a behavioural trait a personality trait, do personalities have the potential to respond to direct or indirect selection, and whether personalities and behavioural syndromes that have been measured over short time scales are stable and can evolve.

First, the repeatability of boldness was low in comparison with other published estimates for personality traits (Bell *et al.*, 2009, though see Dubuc-messier *et al.*, 2016). Whether boldness is a personality trait is a valid question, and to answer this requires a clear definition of a personality trait. A behavioural trait can be classed as a personality trait when it is stable across contexts and/or time, indicating a long-term element to the behaviour, which is demonstrated with repeatability. Repeatability across years indicates, arguably, the underlying personality of the adult individual, though personality is known to shift as individuals develop and age (Roberts & Mroczek, 2008; Groothuis & Trillmich, 2011). Behaviour in social contexts is a mixture of the individual's personality and their reaction to the specific social partners and context (Niemelä & Santostefano, 2015), making personality harder to determine. Consistent behaviour can affect fitness and thus heritable and non-heritable personality traits are ecologically relevant.

By being significantly repeatable across years, boldness in wild house sparrows has passed the statistical threshold for personality. Yet boldness was not repeatable within years because of within-year habituation and the influence of the partner (see Text S3 and Table S2). Thus, boldness appears stable over long periods of time, demonstrations of which are rare (though see work by e.g. Class &

Brommer, 2015). It is difficult to balance gaining sufficient numbers of behavioural assessments and characterising the long-term, immutable portion of an individual's behaviour for individuals in the wild, and it is not always clear whether short-term assessments capture stable personality traits (Biro, 2012; Edwards *et al.*, 2013). This study is one of few that has monitored behaviours in the wild over years and not weeks or months, enabling us to separate short-term effects from more stable aspects of behaviour. Our low but significantly repeatable traits are supporting evidence for a lifelong stable element to behaviour. Further work could investigate the contexts and time-frames over which personality traits become biologically meaningful.

We found large variation in the heritability of behavioural traits: the heritability of exploration was relatively high (Table 2), yet the heritability of nestling activity was close to zero (Table 2) and was only significant after the inclusion of fixed effects (Table S4). This is in contrast to more stable morphological traits measured in this house sparrow population (Teplitsky *et al.*, 2014), and published estimates of heritability of activity across taxa (Oers & Sinn, 2013). Our statistical power is sufficient to detect strong to moderate additive genetic effects for nestling activity and adult exploration, therefore we think that these results are reliable (Text S2), and it is therefore likely that, for adult exploration behaviour, the additive genetic effect contributes strongly to personality. Such variable heritability is a good indicator that these traits have the potential to vary in their strength of response to selection, though the adult traits do not appear to be under selection in the years studied. Thus, whilst these personality traits have variable potential to respond to selection, direct selection on personality via productivity in a year was not detectable .

There are several reasons why our personality traits might not be heritable. A trait could be highly plastic, such that the mechanism of plasticity could be stable and heritable rather than the trait mean (i.e. heritable reaction norm rather than heritable personality Nussey *et al.*, 2007; Dingemanse *et al.*, 2010, 2012). In a wild population of great tits, *Parus major*, both personality and plasticity were heritable based on social pedigree information (Araya-Ajoy & Dingemanse, 2017), though in the absence of genetic parentage and cross-fostering, heritabilities can be less accurate due to extra-pair paternity, and are likely to be confounded with maternal effects. Whilst large sample sizes are needed to investigate the heritability of plasticity (Martin *et al.*, 2011; van de Pol, 2012), understanding this might reveal whether plasticity drives between-individual differences in personality, how personality traits can be unstable and still evolve (i.e. whether it is plasticity that evolves), and how personality traits are physiologically regulated.

One cause for plasticity could be the social environment and associated biotic and abiotic factors. In support of this, we found that nestling activity was more similar within social broods than between broods (Table 2, also when fixed effects were included, Table S2). Boldness was similar within social pairs (effect of shy partner on own boldness: -0.74 ± 0.12, Table S2), though note that social effects cannot be distinguished from assortative mating within our dataset and would be a good hypothesis to test. Evidence for social effects on personality is mounting (Carter *et al.*, 2012; Courtene-Jones & Briffa, 2014; Mahr *et al.*, 2015). Niemelä and Santostefano (2015) argue that social interactions can change personality over short and long timescales, and the latter could lead to indirect genetic effects of one individual on those that it interacts with (Bijma, 2014; Wilson, 2014). Indirect genetic effects can speed up or slow down the response to selection (Wilson, 2014; Niemelä & Santostefano, 2015). Clearly both an individual's behavioural traits and the selection on these traits can be altered within and by social contexts, complicating the measures of both trait and selection.

We found no behavioural syndrome, which contrasts with meta-analytic correlations between these traits (Garamszegi *et al.*, 2012, 2013). However, this is not surprising in the context of our study for three main reasons. First, the strongest syndromes are found within the same test environment (Garamszegi *et al.*, 2013) and could be stronger over short timescales (Wuerz & Krüger, 2015). We found no syndrome in traits measured across test environments and over a long period of time. Thus, it remains to be shown whether some syndromes are independent of the test environment and are temporally stable. Second, syndromes might only form in response to specific selection pressures on a population. For example, in brown trout *Salmo trutta* and three-spined stickleback *Gasterosteus aculeatus*, predators removed specific behavioural phenotypes and induced plastic changes in the remaining individuals, leading to behavioural syndromes (Bell & Sih, 2007; Adriaenssens & Johnsson, 2013). In support of this, behavioural syndromes in wild-caught individuals disappeared in the laboratory (Hedrick & Bunting, 2013). Predator-based selection might be less consistent and environmental heterogeneity might be lower in our population, so that no correlation is created between traits. Third and last, selection pressures on a given syndrome structure might vary between life-history stages, leading to correlations between behavioural traits within but not between life-history stages (Wolf *et al.*, 2007; Groothuis & Trillmich, 2011; Chan & Kim, 2014), as supported by empirical work (Hedrick & Kortet, 2011; Kluen & Brommer, 2013). Wuerz and Krüger (2015) show that personality traits can remain stable through ontogeny but behavioural syndromes can break down, and Ballew et al. (2017) show that selection pressures on the same behaviour can vary between juvenile and adult stages. More study on the stability of behavioural syndromes and the selection pressures generating them in the wild would be a challenging but informative goal for the future.

In conclusion, the heritability of personality is variable between traits, and our results imply that other personality traits could potentially show varying responses to selection. None of the personality traits in this study were correlated (i.e. there was no behavioural syndrome), and the adult traits were not under detectable selection. We displayed a comprehensive array of repeatabilities and heritabilities for three behavioural traits measures over a longer time span and more powerful pedigree than most other wild studies of personality. As more field studies like ours accumulate, these will reveal how the phenotypic and genetic basis of personality, and thus the potential of personalities to respond to selection, is maintained. This information will aid in clarifying whether personality traits differ in heritability because they have different evolutionary purposes and functions, or because our concept of stable personalities needs revising (Carter *et al.*, 2013).

Supporting Information

Text S1: Additional Methods

Text S2: Power Analysis

Text S3: Fixed Effects

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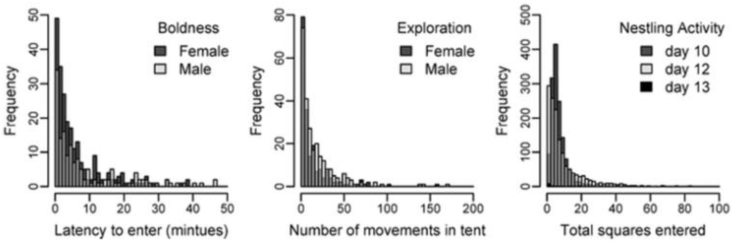
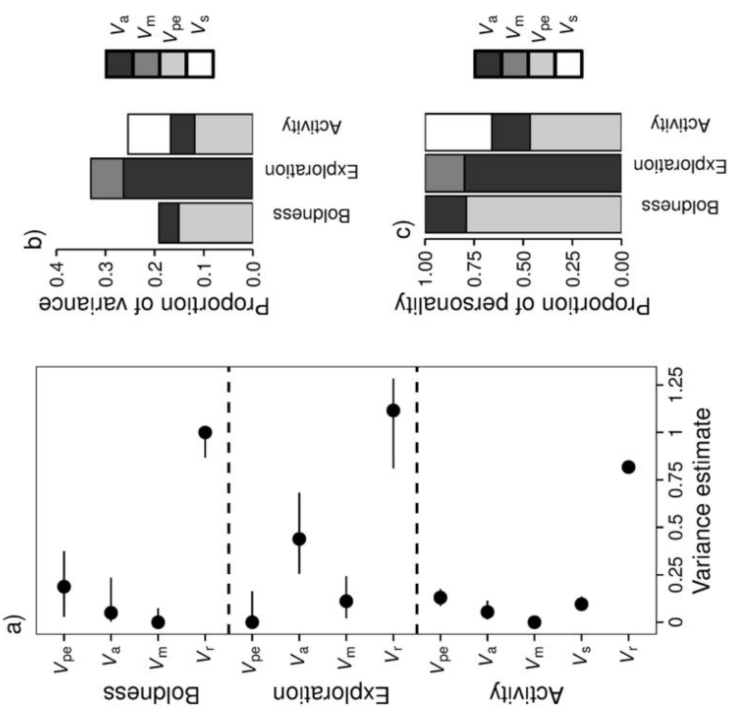
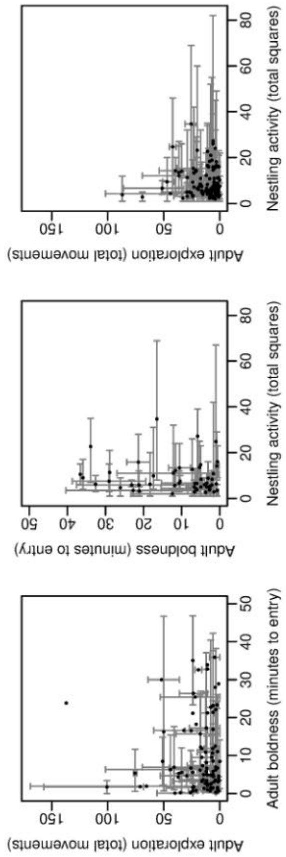
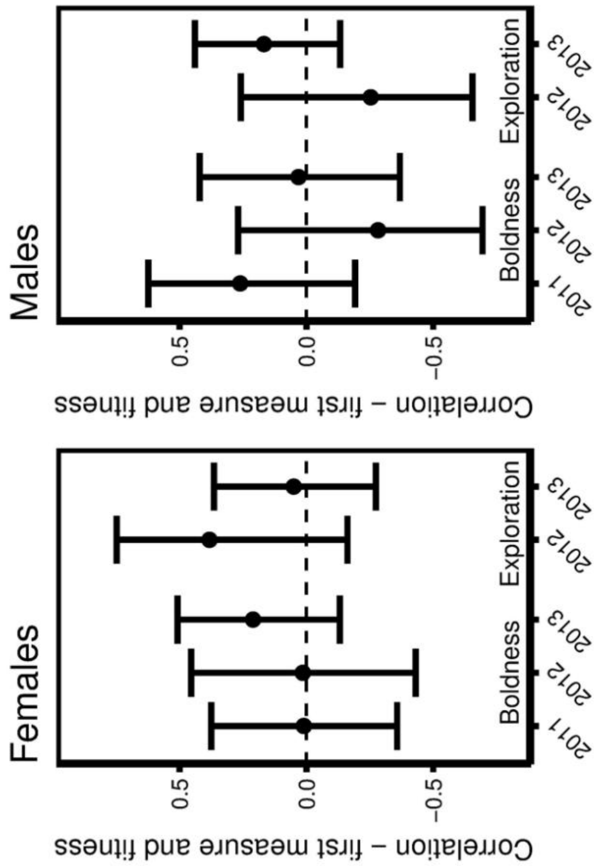

Boldness
■ Female
□ Male
Frequency
0
10
20
30
40
50
0
10
20
30
40
50
Latency to enter (mintues)
Exploration
■ Female
□ Male
Frequency
0
20
40
60
80
0
50
100
150
200
Number of movements in tent
Nestling Activity
■ day 10
□ day 12
■ day 13
Frequency
0
100
200
300
400
500
0
20
40
60
80
100
Total squares entered


a)
Boldness
V_{pe}
V_a
V_m
V_r
Exploration
V_{pe}
V_a
V_m
V_r
Activity
V_{pe}
V_a
V_m
V_s
V_r
0
0.25
0.5
0.75
1
1.25
Variance estimate
b)
Proportion of variance
0.0
0.1
0.2
0.3
0.4
Boldness
Exploration
Activity
V_a
V_m
V_{pe}
V_s
c)
Proportion of personality
0.00
0.25
0.50
0.75
1.00
Boldness
Exploration
Activity
V_a
V_m
V_{pe}
V_s


Adult exploration (total movements)
0
50
100
150
Nestling activity (total squares)
0
20
40
60
80
Adult boldness (minutes to entry)
0
10
20
30
40
50
Nestling activity (total squares)
0
20
40
60
80
Adult exploration (total movements)
0
50
100
150
Adult boldness (minutes to entry)
0
10
20
30
40
50


Females
Males
Correlation – first measure and fitness
0.5
0.0
−0.5
Boldness
Exploration
2011
2012
2013