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

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4 Bert Thys[a*], Marcel Eens[a], Silke Aerts[a], Amandine Delory[a], Arne Iserbyt[a], Rianne Pinxten[a,b]

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6 [a]Department of Biology, Behavioural Ecology and Ecophysiology Group, University of

7 Antwerp, Wilrijk, Belgium

8 [b]Faculty of Social Sciences, Antwerp School of Education, University of Antwerp, Antwerp,

9 Belgium

15 [*]Correspondence: B. Thys, Campus Drie Eiken, Building D–Room 1.23, Universiteitsplein 1,
16 2610 Antwerp (Wilrijk), Belgium
17 E-mail address: bert.thys@uantwerpen.be
18

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20 Personality traits and behavioural syndromes are often assumed to relate to life history

21 strategies and lifetime fitness variation and hence may be generally under selection. Key in this

22 regard is the, often untested, assumption that individual differences in (correlated) behaviours

23 are maintained across contexts and over an individual's lifetime. Here, we tested this

24 assumption, using a population (N=30) of captive male starlings, *Sturnus vulgaris*, a highly

25 gregarious avian species. We repeatedly assayed novel environment exploration and different

26 aspects of sociability towards a female conspecific, across seasonal contexts (spring and

27 autumn) and across a 2-year period, which represents a substantial portion of a starling's life

28 span. We found that, regardless of plasticity at the population level, both exploration behaviour

29 and sociability traits investigated were moderately repeatable across seasons and years, with no

30 significant differences between repeatability estimates over different timescales. However, no

31 evidence was found for significant between-individual correlations between the investigated

32 traits, including different aspects of sociability. Taken together, our results provide empirical

33 evidence that exploration and sociability are personality traits that are stable across seasons and

34 in the long term but do not form behavioural syndromes. Given the recent evidence that

35 personality traits are often heritable, the traits assessed in our study might have the potential to

36 evolve independently under selection. This long-term consistency in exploration and sociability

37 might have important implications for the social organization within complex social

38 environments and influence a wide variety of ecologically relevant processes.

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40 KEY WORDS: animal personality; behavioural syndrome; social behaviour; long term;

41 seasonal context; (co)variance partitioning; *Sturnus vulgaris*

42   Across a variety of animal taxa, individuals within populations often display remarkable

43   differences in behavioural tendencies that are consistent across time and contexts (Gosling,

44   2001; Sih, Bell, & Johnson, 2004; Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Such

45   consistent (i.e. repeatable) individual differences in average behaviour are referred to as

46   'personality' (Dingemanse, Kazem, Réale, & Wright, 2010; Garamszegi & Herczeg, 2012), and

47   different personality traits are often observed to covary among individuals, forming so-called

48   behavioural syndromes (Sih et al., 2004). However, behaviour is inherently plastic and thus

49   (co)varies within individuals (Bell, Hankison, & Laskowski, 2009; Dingemanse et al., 2010).

50   One therefore needs to partition the raw phenotypic (co)variation, from repeated measurements

51   on individuals, into its within- and between-individual components (see Dingemanse &

52   Dochtermann, 2013).

53   Despite increasing research interest, explaining the existence and maintenance of

54   personality variation remains puzzling (e.g. Dingemanse & Wolf, 2010; Réale, Dingemanse,

55   Kazem, & Wright, 2010). Nevertheless, growing evidence suggests that personality traits are

56   heritable, linked with life history traits and lifetime fitness variation (e.g. Biro & Stamps, 2008;

57   Smith & Blumstein, 2008; Dochtermann, Schwab, & Sih, 2015), and hence might be maintained

58   by life history trade-offs (e.g. Wolf, Van Doorn, Leimer, & Weissing, 2007). These

59   observations have been integrated into the pace-of-life syndrome (POLS) hypothesis,

60   suggesting the coevolution of physiology, personality and life history (Réale, Garant, et al.,

61   2010). However, if long-term selection results in the coevolution of personality and life history

62   traits, one key assumption is that individual differences in (correlated) behaviours are

63   maintained over considerable portions of a species' lifetime (Réale, Garant, et al., 2010; Stamps

64   & Groothuis, 2010; Brommer & Class, 2015). Similarly, these individual differences are

65   expected to be maintained across ecologically relevant contexts (e.g. predation pressure,

66   photoperiod or reproductive seasons; Dingemanse et al., 2010). To date, surprisingly little is

67   known about the extent to which consistent behavioural differences are maintained across

68   seasons and over long periods of time (but see David, Auclair, & Cézilly, 2012; Kluen &

69   Brommer, 2013; Class & Brommer, 2015; Wuerz & Krüger, 2015). Explicitly addressing these

70   questions is crucial, ultimately because they have important implications for our understanding

71   of the development, ecological significance and evolutionary potential of personality traits and

72   behavioural syndromes (Réale et al., 2010; Stamps & Groothuis, 2010; Brommer & Class,

73   2015).

74   One behavioural trait commonly found to be consistent is exploration behaviour in a

75   novel environment (e.g. great tits, *Parus major*: Dingemanse, Both, Drent, van Oers, & Van

76   Noordwijk, 2002; European starlings, *Sturnus vulgaris*: Minderman, Reid, Evans, &

77   Wittingham, 2009; zebra finches, *Taeniopygia gutatta*: Schuett & Dall, 2009; house sparrows,

78   *Passer domesticus*: Mutzel, Kempenaers, Laucht, Dingemanse, & Dale, 2011; fairy-wrens,

79   *Malurus cyaneus*: Hall et al., 2015). This aspect of personality is often observed to be part of a

80   behavioural syndrome including boldness, activity and aggression (see Garamszegi, Markó, &

81   Herczeg, 2013). Another trait termed sociability, defined as an individual's nonaggressive

82   behavioural response to conspecifics, might also constitute an aspect of personality (Réale et

83   al., 2007). In highly gregarious species, sociability refers to a broad trait category encompassing

84   a range of social behaviours (e.g. tendency to seek proximity to conspecifics, sexual behaviour

85   towards opposite-sex conspecifics, affinitive behaviour, etc.; Cote & Clobert, 2007; Schuett &

86   Dall, 2009; Koski, 2011). Despite growing interest in the influence of the social environment

87   on personality, and vice versa (see Webster & Ward, 2011; Wolf & Krause, 2014), studies

88   investigating which types of social behaviour represent aspects of personality are limited (but

89   see Cote & Clobert, 2007; Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010; Koski, 2011;

90   Aplin et al., 2015). Insights into the consistency of individual differences in sociability are

91   important, especially in gregarious species (see Koski, 2014), since they are likely to play an

92 important role in interactions within complex social environments, might be shaped by sexual

93 selection under certain conditions, and might influence behavioural strategies and ultimately

94 fitness (e.g. Cote, Dreiss, & Clobert, 2008; McGhee & Travis, 2010; Oh & Badyaev, 2010;

95 Formica et al., 2012; Farine & Sheldon, 2015). Consistent individual differences in sociability

96 are hence expected to be integrated within a general pace-of-life syndrome (POLS); with slow,

97 more thorough explorers being on average more social than fast, superficial explorers (Réale,

98 Garant, et al., 2010). To date, this specific relationship largely remains untested (Budaev, 1997;

99 Haage, Bergvall, Maran, Kiik, & Angerbjörn, 2013; McCowan, Mainwaring, Prior, & Griffith,

100 2015).

101 Here, we integrated some largely overlooked aspects and hypotheses in the personality

102 literature using the European starling, a highly gregarious hole-nesting species with complex

103 social behaviour (Feare, 1984; Eens, 1997). Specifically, we (1) integrated different aspects of

104 sociability (time spent near a female conspecific and near the provided nestbox in the presence

105 of a female), in addition to novel environment exploration behaviour, within a personality

106 framework and (2) tested the POLS hypothesis' proposed negative relationship between

107 exploration and sociability traits (Réale, Garant, et al., 2010). Simultaneously, we explicitly

108 investigated (3) whether behavioural repeatability and behavioural syndrome structure between

109 these traits varied across seasonal contexts (spring and autumn) and/or across years. If between-

110 individual differences in (correlated) behaviours are maintained across seasons and years this

111 would suggest their (correlated) evolutionary response to selection.

112 <H1>METHODS

113 *<H2>Ethical note*

114 All experiments undertaken in this study complied with ethical guidelines of the

115 University of Antwerp and Flemish and European laws regarding animal welfare, and adhere

116 to the ASAB/ABS guidelines for the use of animals in behavioural research and teaching.

117 Specifically, permission to capture starlings from the wild and house them in captivity (in

118 approved facilities) was granted by the Flemish administration (Agentschap voor Natuur en

119 Bos, ID numbers ANB/BL-FFN 08-11344 and ANB/BL-FFN 12-00381). Behavioural assays

120 were approved by the ethical committee of the University of Antwerp (ID number 2011-31).

121 Neither procedure adversely affected the starlings in the short term or for the overall period of

122 the study. After each test session (see below), birds were returned to their holding conditions.

123 *<H2>Subjects*

124 Thirty juvenile males, judged from their plumage characteristics (Svensson, 1984), were

125 caught from the wild at several sites around Antwerp, Belgium (51°13'N, 4°24'E), in October

126 2008. From then onwards all males were held captive under the same standardized conditions

127 in a single large outdoor aviary (16 x 6 m and 2.5 m high) equipped with several perches, at the

128 University of Antwerp campus in Wilrijk, Belgium. Starlings can be kept easily in captivity,

129 where they show normal social and reproductive behaviour (Eens, Pinxten, & Verheyen, 1990;

130 Eens, Pinxten, & Verheyen, 1993). Upon introduction into this aviary, males were ringed with

131 a numbered metal ring and a unique combination of plastic colour rings, allowing easy

132 identification. Food (mixed 1/3 Orlux UniPatee, Orlux, Belgium and 2/3 Merelkorrel Speciaal,

133 Nifra–Van Camp, Belgium) was provided ad libitum, and birds had unrestricted access to

134 drinking and bathing water.

135 *<H2>Test room*

136 The test room (Fig. 1) was a modified version of one used to quantify exploration

137 behaviour in great tits (Verbeek, Drent, & Wiepkema, 1994; Dingemanse et al., 2002). It was a

138 wooden structure (2.95 x 2 and 2.5 m high) with a closed roof, three blind white walls and wire-

139 mesh front wall. A wooden 'start box' (24 x 14 cm and 14 cm high) was connected to the test

140   room via an entrance hole (diameter = 5 cm) at a height of 1.6 m, allowing birds to enter the

141   room without further handling. Inside the test room there were nine 'items': five perches, a

142   shelf, a food dish, a small cage and the wire mesh. A small wire cage (24 x 16 cm and 22 cm

143   high) next to perch 4 was present for the sociability assay (see below). Furthermore, a nest hole

144   (diameter = 5 cm) at a height of 1.1 m, close to perch 5, was connected to a nestbox attached at

145   the outside of the room. Given that starlings also explore the ground during exploration tests

146   (Minderman et al., 2009), the ground was covered with sand and provided with two strips of

147   grass (2.95 x 0.4 m), one on each side, dividing the ground into three distinct parts. Observations

148   were made by a single observer in a darkened hide behind a one-way screen and all trials were

149   videotaped (Sony Handycam HDR-XR550E/XR550VE).

150   ### <H2>Behavioural assays

151   ### <H3>General procedure

152   Over a 2-year period (2011 and 2013), all males took part in four exploration trials and

153   three sociability trials (Table 1), and were kept and handled in the same standardized conditions.

154   Two days before the start of each session, all males were caught from the large aviary and

155   randomly allocated to six identical smaller outdoor aviaries (3.2 x 2 m and 2.5 m high), where

156   they were housed in groups of five and provided with food and water ad libitum. The day before

157   the behavioural assays, all birds from each small aviary were weighed and transported to

158   individual cages (100 x 30 cm and 40 cm high), located in two separate outdoor aviaries,

159   identical to the small outdoor aviaries in which they were housed. The next day, each bird was

160   caught from his individual cage (random but alternately between aviaries) and placed in the

161   completely opaque start box connected to the test room (Fig. 1).

162   ### <H3>Exploration assay

163   After the male had spent 5 min in the start box for acclimatization, the entrance hole

164   giving access to the test room was opened by lifting a slide and the time it took the bird to enter

165   the room (latency) was recorded. If the bird had not entered the test room by itself (spontaneous

166   enter) after 1 min, it was encouraged to do so by briefly lifting the outside entrance of the start

167   box (forced enter), and subsequently appointed a maximum latency of 60 s. As males either

168   spontaneously entered within 10 s (52% of the trials) or had a maximum latency of 60 s (36%

169   of the trials), latency was transformed into a binary variable (i.e. spontaneous versus forced

170   enter).

171   The exploration trial started once the bird entered the room and lasted for 15 min, during

172   which the following behavioural parameters were recorded (see also Minderman et al., 2009):

173   (1) number of unique items visited (maximum 12, see Fig. 1), (2) total number of visits to items

174   and (3) total number of flights. As, in contrast to Minderman et al., (2009), the observed

175   variation in the time spent on the ground was low in our study population, and particularly

176   during the first trial (with only one male visiting the ground), we scored the different parts of

177   the ground (i.e. grass 1, grass 2 and sand; Fig. 1) as three additional items and not as separate

178   exploration parameters.

179   *<H3>Sociability assay*

180   Sociability trials immediately followed the 15 min exploration trials, except in spring

181   2011 when the sociability trial followed approximately 7 days after the second exploration trial

182   (Table 1). However, males were allowed to explore the room for 5 min preceding the sociability

183   trial in spring 2011. In total, 13 different stimulus females were used, i.e. three, four and six

184   different females for trial 1, 2 and 3, respectively. The same female was never used for two

185   consecutive trials on the same day. Sociability trials started by dimming the light in the test

186   room and placing a single stimulus female into the small cage via a slide from outside (Fig. 1).

187   Trials lasted 15 min after the lights were turned on again. During these trials, behavioural

188   parameters associated with the male's response towards female conspecifics were recorded

189   (Eens et al., 1990; Eens et al., 1993; Gwinner, Van't Hof, & Zeman, 2002; Pinxten, De Ridder,

190   & Eens, 2003): time spent in proximity to the female (Time FE) and time spent near the nestbox

191   (Time NB).

192   One commonly assessed component of sociability is the tendency to seek proximity to

193   conspecifics, referred to as 'social tendency' (e.g. Budaev, 1997; Cote & Clobert 2007;

194   McEvoy, While, Sinn, Carver, & Wapstra,, 2015). As a measure of this tendency we quantified

195   Time FE, referring to the sum of the time spent on the small cage in which the female was

196   placed and on the perch near the small cage (perch 4). During the breeding season (i.e. spring),

197   male starlings having access to a nest hole may respond to the presence of a conspecific female

198   by showing mate attraction behaviour, i.e. trying to attract the female to this nest hole by sitting

199   close to it, hanging in the nest hole or by entering it (Eens et al., 1993; Gwinner et al., 2002).

200   Furthermore, during the nonbreeding season (e.g. autumn) there may be competition between

201   (captive) starlings for access to a nest hole to roost (Pinxten, De Ridder, De Cock, & Eens,

202   2003). We therefore quantified Time NB, referring to the sum of the time spent hanging in the

203   nest hole, on the perch near the nest hole (perch 5) and in the nestbox. Time NB is thus assumed

204   to indicate the investment in mate attraction (spring) or competition (autumn) in response to the

205   presence of the female. Moreover, including Time FE and Time NB as separate parameters

206   allowed us to assess the relative investment in, and relation between, both measures of

207   sociability. As we were also interested in the relation between exploration and the overall

208   response towards a female, we included a composite measure of sociability (Time TR),

209   calculated as the sum of Time FE and Time NB. All three measures, which we refer to as

210   sociability traits, were expressed as proportional times, relative to the total duration of the trial.

211   *<H2>Statistical analyses*

212   All analyses were performed in R 3.1.0 (R Core Team, 2014). Prior to analyses, Time

213   NB and Time FE were square-root transformed to meet the normality of residuals assumption

214   in linear models, and all three sociability traits were standardized (Schielzeth 2010). The three

215   parameters that quantified exploration were log-transformed, standardized and entered in one

216   overall principal component analysis (PCA). This PCA resulted in a single principal component

217   (eigenvalue = 2.85) explaining 95% of the variance, with strong positive loadings for all

218   parameters, i.e. number of unique items visited (0.568), total number of visits to items (0.586)

219   and number of flights (0.578). This principal component, referred to as 'Expl (PC)', was used

220   in all further analyses as an overall measure of exploration behaviour.

221   *<H3>Univariate mixed models*

222   Univariate mixed models (MMs) were used to investigate the influence of potential

223   covariates and factors on each of the behavioural traits. Separate univariate MMs were fitted

224   (lmer function, package lme4; Bates, Mächler, Bolker, & Walker, 2015) with Gaussian error-

225   distribution and included random intercepts for male identity (ID). Context (spring versus

226   autumn) and year (2011 versus 2013) were included as fixed effects in all models. Furthermore,

227   body mass and time of day were centred within individuals (van de Pol & Wright, 2009) and

228   both within- and between-individual components were added as fixed effects in all models. The

229   model for Expl (PC) also included the factor latency (spontaneous versus forced enter) as a

230   fixed effect. Stepwise backward elimination of nonsignificant terms, starting with the least

231   significant, was used to obtain minimum adequate MMs. To explore the overall effect of female

232   identity on male response, a likelihood ratio test (LRT) between the mixed models for Time TR

233   with and without Female ID as extra random effect was performed (Zuur, Ieno, Walker,

234   Saveliev, & Smith, 2009).

235   Furthermore, because of our unbalanced sampling design (Table 1), separate univariate

236   MMs with a random intercept for ID were used to estimate the short-term and long-term

237   repeatability of Expl (PC). All other repeatabilities (for both exploration and sociability traits)

238   were estimated from the multivariate MMs. The sim function (package arm; Gelman et al.,

239   2015) was used to simulate values of the posterior distribution of all model parameters and we

240   considered effects significant when credible intervals (CrI) did not overlap zero. Fixed effects

241   found to be nonsignificant in the univariate MMs were omitted in further multivariate MMs.

242   *<H3>Multivariate mixed models*

243   To partition (co)variances we applied multivariate MMs using the MCMCglmm

244   package (Hadfield, 2010), which relies on Markov Chain Monto Carlo sampling to estimate

245   parameters. A prior distribution (V = diag(4), ν = 1.004) was used throughout, and chains were

246   run for 1.3 million iterations, with a burn-in phase of 300 000 and a thinning interval of 1000

247   iterations. The use of a range of alternative prior specifications (e.g. default) did not affect the

248   results qualitatively. Convergence and mixing of models was assessed by visually checking

249   traces of posterior distributions over iterations and Gelman–Rubin statistics among chains

250   (Gelman & Rubin, 1992; potential scale reduction factor < 1.1 for all parameters).

251   Autocorrelation within chains was < 0.07 for all parameters (Hadfield, 2010), indicating all

252   model assumptions were met. All multivariate analyses were run with the average of the

253   individual PC-scores of the first two exploration trials, resulting in a single exploration score

254   per male for the spring of 2011.

255   We ran three multivariate MMs, using different (sub)sets of data which included the

256   repeated measurements relevant for the period of interest, i.e. overall (three repeats), across-

257   season (spring 2011–autumn 2011) and across-year (spring 2011–spring 2013) data sets. All

258   models, with the four behavioural traits as response variables, were fitted assuming multivariate

259   Gaussian error distribution and included the fixed effects found to be significant in the

260   previously described univariate MMs. Hence, all behavioural traits, including the three

261   sociability measures, were modelled as separate traits, but this assumption was explicitly

262   examined by calculating the between- and within-individual correlations between them (see

263   Baugh, van Oers, Dingemanse, & Hau, 2014 for a similar approach).

264   In each multivariate model we included male ID as random intercept, allowing the

265   partitioning of the multivariate phenotypic (co)variances (not explained by the included fixed

266   effects) into its between- and within-individual components. Adjusted repeatabilities for each

267   of the traits were then estimated as the between-individual variance (V_I) divided by the total

268   phenotypic variance (i.e. sum of V_I and within-individual variance V_R; Nakagawa & Schielzeth,

269   2010). Between- (COV_I) and within- (COV_R) individual covariances between pairs of traits

270   were divided by the square-root of the product of their respective variances to obtain the

271   corresponding between- (r_I) and within- (r_R) individual correlations, respectively (see

272   Dingemanse & Dochtermann, 2013). All results are presented as means with 95% CrI, unless

273   stated otherwise, and were considered significant when CrI did not overlap zero.

274   <H1>RESULTS

275   *<H2>Population level effects*

276   Both season and year had a significant effect on population level exploration (Table 2).

277   Male exploration behaviour was higher in the autumn (0.64 ± 0.36 SE) than in the spring (-0.21

278   ± 0.16 SE) and in 2013 (0.60 ± 0.30 SE) than in 2011 (-0.20 ± 0.18 SE). However, exploration

279   behaviour did not differ on average between the two exploration trials in the spring of 2011

280   (Fig. 2). Adding Female ID as random effect in the mixed model of male total response (Time

281   TR) towards a female did not improve the fit (LRT: $\chi^2_1 = 1.99$, $P = 0.16$), and was removed

282   from further analyses. Furthermore, male total response (Time TR) was significantly influenced

283   by season (Table 2), with males responding on average more to the presence of the female in

284   the autumn (0.56 ± 0.06 SE) than in the spring (0.41 ± 0.05 SE). The overall response of males,

285   however, was not significantly different between years (Table 2, Fig. 3). The time spent near

286   the nestbox (Time NB) was significantly influenced by both season and year (Table 2),

287   indicating that males spent on average more time near the nestbox in the autumn (0.25 ± 0.05

288   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

289   SE; Fig. 3). On the other hand, males spent on average the same amount of time near the female

290   (Time FE), regardless of season or year (Table 2, Fig. 3). None of the other potential covariates

291   and factors had a significant influence on any of the investigated traits (Table 2).

292   *<H2>Short-term, across-season and long-term repeatability*

293   Males showed significant between-individual differences over different timescales for

294   all four investigated behavioural traits, with season and/or year included as fixed effects in the

295   models (Table 3). Male exploration behaviour (Expl (PC)) was consistent over short and long

296   time periods but repeatability was lower across seasons. For male total response (Time TR),

297   across-season repeatability was higher than, although not significantly different from, across-

298   year repeatability. Males differed consistently in the time they spent near the nestbox (Time

299   NB), both across seasons and years. The time males spent near the female (Time FE) was also

300   repeatable, with moderate to low repeatabilities across seasons and years. For all traits, the

301   repeatability estimates did not differ significantly over different time periods and across

302   seasons, as indicated by overlapping CrIs.

303   *<H2>Between- and within-individual correlations*

304   First, overall, exploration behaviour and sociability traits were not observed to covary

305   over any timescale, either between or within individuals (Table 4). However, across spring 2011

306   and spring 2013, exploration showed a tendency to be positively correlated within individuals

307 with both the total response (Time TR) and especially with the time males spent near the

308 nestbox (Time NB; Table 4). This tendency between exploration and Time TR and Time NB

309 was conserved in the overall data set, despite being attenuated by the absent across-season

310 correlation (Table 4).

311   Second, the time males spent near the nestbox (Time NB) and near the female (Time

312 FE) did not covary, either between or within individuals. The total response during the

313 sociability trials (Time TR), on the other hand, was positively correlated both between and

314 within individuals with the time near the nestbox and the time near the female (Table 4).

315   <H1>DISCUSSION

316   We found that novel environment exploration and different aspects of sociability were

317 moderately repeatable across seasons and a 2-year period, representing a substantial part of the

318 adult starling's life span (Feare, 1984). Regardless of population level plasticity for some traits,

319 repeatability estimates did not differ across timescales, indicating that these personality traits

320 are stable in male starlings. However, we found no evidence for significant between-individual

321 correlations (i.e. behavioural syndromes) between exploration and the sociability traits.

322 Moreover, different aspects of sociability did not covary between individuals, and appeared to

323 be independent aspects of male starlings' social personality. In what follows, the potential

324 ecological and evolutionary implications of our findings are discussed.

325   *<H2>Population level plasticity across seasons and years*

326   Novel environment exploration and time spent near the nestbox increased from the

327 spring towards the autumn of 2011 and remained at approximately the same level in the spring

328 of 2013. The average time spent in proximity to the female did not differ between seasons and

329 years. Several studies have reported an increase in exploration with repeated exposure to an

330 'open field' test, assumed to be caused by a reduction in fear with increased habituation (e.g.

331   Budaev 1997; Dingemanse et al., 2002; Minderman et al., 2009). Such habituation effects are

332   expected to be more pronounced on shorter timescales (e.g. Dingemanse et al., 2002). Our

333   findings are not in accordance with this explanation since exploration only increased between

334   the trials with the longest intertrial intervals (Fig. 2). Unfortunately, data were not available (no

335   repeated measurements within seasons and years, e.g. Boulton, Grimmer, Rosenthal, Walling,

336   & Wilson, 2014) to disentangle habituation and experience effects from season and year effects,

337   and their relative contributions in explaining our results therefore remains unresolved.

338   One interesting possibility is that males become more exploratory and spend more time

339   near the nestbox as they develop. Indeed, life history theory predicts that individuals take more

340   risk and invest more in reproduction with age as their future fitness expectations decrease (e.g.

341   Stearns, 1989; Roff & Fairbrain 2007). Our observation that males spent more time near the

342   nestbox in the second, relative to the first, spring is in line with these predictions (e.g. Gwinner

343   et al., 2002). At present, this remains speculative and age-related effects at the population level

344   (and individual/genetic level; see Brommer & Class, 2015) deserve more empirical attention

345   (see Class & Brommer, 2016 and references therein).

346   *<H2>Behavioural repeatability*

347   Exploration and sociability traits were moderately repeatable across seasons and years

348   (range 0.25–0.41). Given that repeatability is generally thought to set an upper limit to

349   heritability (Boake, 1989; but see Dochtermann, et al., 2015), our findings suggest that these

350   traits have a genetic basis and hence the potential to evolve under selection, although this merits

351   further study, implementing a quantitative genetic approach (e.g. Boake, 1989; Réale &

352   Dingemanse, 2012; Dingemanse & Dochtermann, 2014). Interestingly, repeatability estimates

353   did not decrease with increasing intertrial intervals (Bell et al., 2009), indicating that between-

354   individual variation for these particular traits in this species was not affected by seasonal context

355   and remained consistent over substantial parts of the life span. So regardless of population level

356   plasticity for some traits (see above), individual differences were maintained and stable.

357   The long-term maintenance of consistency is one of the key assumptions within theories

358   linking personality and life history strategies (cf. POLS, Réale, Garant, et al., 2010; see also

359   Wolf et al., 2007). In great tits, for example, consistent and heritable individual differences in

360   exploration behaviour have been linked to survival and offspring recruitment (review in

361   Dingemanse & Réale, 2005), and individuals have been shown to adjust their exploration

362   behaviour in relation to their future survival prospects (Nicolaus et al., 2012). This suggests that

363   life history trade-offs might be key in explaining the adaptive evolution of personality (see also

364   Dammhahn, 2012; Niemelä, Vainikka, Hedrick, & Kortet, 2012; Hall et al., 2015). At present,

365   little is known about exploration behaviour in starlings, but a few studies indicate that aspects

366   of exploration in the laboratory are related to circulating hormone levels (Apfelbeck & Raess,

367   2008), learning performance (Boogert, Reader, & Laland, 2006), environmental sensitivity

368   (Minderman et al., 2009) and home range size in the wild (Minderman et al., 2010), indicating

369   its ecological relevance. Our findings are in line with recent empirical studies revealing long-

370   term consistency in exploration behaviour (Koski, 2011; David et al., 2012; Hall et al., 2015;

371   Wuerz & Krüger, 2015). Together, this suggests that exploration behaviour is an ecologically

372   relevant, long-term stable personality trait in a variety of species that is shaped by selection and

373   associated with differences in life history.

374   Similarly, long-term consistency in sociability is likely to be affected by selection and

375   to influence life history trade-offs, especially in highly gregarious species (e.g. Oh & Badyaev,

376   2010; Formica et al., 2012; Koski, 2014; Farine & Sheldon, 2015). We found that male starlings

377   differed consistently in their social tendency (Time FE), in line with findings in other studies

378   (e.g. Cote et al Clobert, 2007; Cote et al., 2010; Koski, 2011; Aplin et al., 2015). Differences

379   in this tendency are known to be functionally significant, as they influence dispersal (Cote &

380   Clobert, 2007; Cote et al., 2010), disease transmission (Hamede, Bashford, McCallum, & Jones,

381   2009), competition for breeding territories (Farine & Sheldon, 2015) and reproductive success

382   (Oh & Badyaev, 2010; Formica et al., 2012; see Koski 2011 for review of primate and human

383   studies). Moreover, male starlings also differed consistently in the time they spent near the

384   nestbox (Time NB). In spring, Time NB is assumed to reflect differences in the investment in

385   mate attraction ('nestbox advertisement'), and hence is likely to influence the reproductive

386   success of male starlings (Pinxten & Eens, 1990; Gwinner et al., 2002). The apparent influence

387   of long-term consistency in social behaviours on a wide variety of ecologically relevant

388   processes and ultimately fitness suggests that life history trade-offs favour their adaptive

389   evolution (Wolf et al., 2007; Réale, Garant, et al., 2010).

390   Another possibility is that long-term consistency in (correlated) social behaviours

391   evolved because it makes individuals predictable in certain types of social interactions (see

392   Wolf, Van Doorn, & Weissing, 2011). Interestingly, we found that individual differences in the

393   time spent near the nestbox were maintained across seasons, even though this is assumed to

394   reflect functionally different behaviours in different seasons (e.g. Eens et al., 1990; Pinxten, De

395   Ridder, De Cock, et al., 2003). One might therefore argue that mate attraction behaviour in the

396   breeding season and competition behaviour outside the breeding season represent a behavioural

397   syndrome (sensu Stamps & Groothuis, 2010). Such a suite of social behaviours might have

398   resulted from correlational selection, hence making an individual's social behaviour predictable

399   across social contexts (i.e. mating and competition; Sinervo & Svensson, 2002; Wolf et al.,

400   2011). Variation in both traits is also likely to relate to social dominance, affecting competition

401   for resources (e.g. nest location or roosting place; see Feare, Gill, McKay, & Bishop, 1995;

402   Witter & Swaddle, 1995; Gwinner et al., 2002). This might have important implications for

403   access to potential mates and social organization within more complex social environments

404   (e.g. Pike, Samanta, Lindström, & Royle, 2008; McGhee & Travis, 2010; Oh & Badyaev, 2010;

405   Wolf & Krause, 2014). One interesting step forward would therefore be to investigate how the

406   observed long-term consistent individual differences in mate attraction behaviour, competition

407   and possibly dominance interact in determining fitness and life history trade-offs within flocks.

408   *<H2>Between- and within-individual correlations*

409   Despite their moderate repeatability across seasons and years, exploration behaviour

410   and sociability traits did not covary between individuals. The absence of significant correlations

411   might be due to a lack of power associated with our modest sample size and number of repeated

412   measurements per individual (see Dingemanse & Dochtermann, 2013). Our results should

413   therefore be interpreted with some caution and future studies should aim to obtain larger sample

414   sizes. Bearing this in mind, our findings suggest that exploration behaviour and the sociability

415   traits investigated do not constitute behavioural syndromes in our population of male starlings.

416   Since there is substantial evidence that phenotypic correlations are generally informative about

417   the sign and magnitude of underlying genetic correlations and hence evolutionary implications

418   (see Dochtermann, 2011; Dochtermann & Dingemanse, 2013), our results suggest that the

419   investigated traits might have the potential to evolve independently from each other (Roff &

420   Fairbrain, 2007), which merits further investigation.

421   The few studies investigating behavioural syndromes between sociability and other

422   personality traits have provided mixed results, with some studies finding no relationship (Haage

423   et al., 2013; McEvoy et al., 2015; our study) and others reporting positive associations (Budaev,

424   1997; McCowan et al., 2015). There are at least two potential reasons for this apparent

425   discrepancy. First, from an evolutionary perspective, if behavioural syndromes arise as a result

426   of adaptive evolution in response to local selection pressures, they might not be present in all

427   species, or populations of the same species (see e.g. Dingemanse et al., 2007; Garamszegi,

428   Markó, & Herczeg, 2012; Garamszegi et al., 2015). Second, from a developmental perspective,

429   if behavioural syndrome structures are not stable across ontogeny or age, they might arise or

430   disappear even within the same (group of) individuals (see e.g. Stamps & Groothuis, 2010;

431   Class & Brommer, 2015; Wuerz & Krüger, 2015). Together, this emphasizes the need for long-

432   term studies investigating different aspects of sociability and their relationships with other

433   personality traits in wild populations experiencing different selective environments (e.g.

434   Stamps & Groothuis, 2010; Class & Brommer, 2015; Garamszegi et al., 2015).

435   Furthermore, we found that different sociability traits (i.e. Time FE and Time NB) did

436   not covary between individuals, indicating they represent independent aspects of male starlings'

437   social personality. Hence, regardless of the above-described potential behavioural syndrome

438   integrating mate attraction and competition (and possibly dominance), social tendency might

439   not be part of this suite of social behaviours. Studies directly addressing relationships between

440   different social personality traits are scarce (see Koski, 2011 for primate and human studies).

441   One recent study in the common waxbill, *Estrilda astrild*, found that social dominance was due

442   to body size rather than social tendency or other personality traits (Funghi, Leitão, Ferreira,

443   Mota, & Cardoso 2015). This indicates that social tendency might not relate to competition and

444   dominance, in line with our findings. It is worth noting here that significant between-individual

445   (as well as within-individual) correlations between Time FE and Time NB on the one hand, and

446   the total time spent responding (Time TR) on the other, are simply the result of the way Time

447   TR is calculated and hence do not represent any biologically meaningful correlations.

448   Interestingly, exploration and time spent near the nestbox tended to positively covary

449   within individuals (while none of the other traits did) across breeding seasons (spring 2011 and

450   spring 2013). Within-individual correlations arise when two (or more) traits change in concert

451   in response to a common environmental (e.g. temperature, predation pressure) and/or internal

452   factor (e.g. hormones; Dingemanse & Dochtermann, 2013). This suggests that when a given

453   individual was more exploratory during an exploration trial it had a higher chance of detecting

454 the nest hole and therefore was more likely to spend time there during the subsequent sociability

455 trial. Although this seems plausible, as by definition, exploration behaviour provides

456 individuals with information about their environment (Renner, 1990), this explanation is not

457 supported by our observations. Indeed, birds were never observed to hang in the nest hole or

458 enter the nestbox during any of the exploration trials. However, we cannot exclude the

459 possibility that individual males differed in other aspects of exploration, such as scanning (see

460 Renner, 1990), potentially causing individual differences in the chance of detecting the nest

461 hole. Nevertheless, our observations indicate that behaviours directed towards the nest hole

462 were solely triggered by the presence of the female, validating Time NB as a measure of social

463 behaviour in starlings (cf. Eens et al., 1990; Eens et al., 1993; Gwinner et al., 2002). Another

464 possibility is that proximate mechanisms such as circulating hormone levels (e.g. testosterone,

465 corticosterone) simultaneously affect the expression of exploration behaviour and nestbox

466 advertisement within individuals, but this largely remains to be tested (but see Pinxten, De

467 Ridder, & Eens, 2003; Apfelbeck & Raess, 2008; Mutzel et al., 2011).

468   In conclusion, our study provides empirical evidence that exploration behaviour and

469 different sociability traits are repeatable across seasons and in the long term, but do not form

470 behavioural syndromes. Given recent evidence that most personality traits are heritable

471 (Dochtermann et al., 2015), this suggests that exploration and sociability traits have the

472 potential to evolve independently in response to selection. However, to adequately understand

473 the ecological and evolutionary significance of these consistent differences, our findings await

474 cross-validation with results from the wild (see Niemelä & Dingemanse, 2014). Subsequently,

475 research into their relation with other behaviours in complex social environments and ultimately

476 fitness will provide insights into how selection might act in maintaining these personality

477 differences.

478

487   **Table 1**. Overview of data collection.

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

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

488

Table 2. Output of univariate mixed models for the total dataset of the four behavioural traits.

	Expl (PC)	Time TR	Time NB	Time FE
Fixed effects	β (95% CrI)	β (95% CrI)	β (95% CrI)	β (95% CrI)
Intercept	**-0.616** **(-1.055 ; -0.152)**	-0.147 (-0.431 ; 0.135)	**-1.057** **(-1.648 ; -0.469)**	0 (-0.256 ; 0.255)
Season[a]	**1.252** **(0.718 ; 1.838)**	**0.422** **(0.082 ; 0.755)**	**0.937** **(0.597 ; 1.292)**	0.218 (-0.149 ; 0.566)
Year[b]	**1.215** **(0.681 ; 1.779)**	0.225 (-0.173 ; 0.631)	**0.557** **(0.214 ; 0.885)**	-0.002 (-0.454 ; 0.440)
Latency[c]	-0.496 (-1.114 ; 0.167)	NA	NA	NA
T of day (a)	-1.559 (-6.740 ; 4.061)	2.315 (-1.855 ; 6.232)	-0.546 (-4.803 ; 3.567)	2.322 (-1.543 ; 6.217)
T of day (w)	-0.640 (-4.630 ; 3.258)	0.337 (-2.240 ; 2.739)	1.801 (-0.476 ; 4.062)	-1.652 (-4.419 ; 0.932)
BM (a)	0.002 (-0.064 ; 0.066)	-0.028 (-0.073 ; 0.016)	-0.015 (-0.058 ; 0.027)	-0.023 (-0.067 ; 0.019)
BM (w)	-0.058 (-0.129 ; 0.016)	0.004 (-0.042 ; 0.048)	0.03 (-0.008 ; 0.071)	-0.030 (-0.082 ; 0.019)
Random effects	β (95% CrI)	β (95% CrI)	β (95% CrI)	β (95% CrI)
ID	0.883 (0.562 ; 1.288)	0.404 (0.261 ; 0.584)	0.384 (0.260 ; 0.555)	0.308 (0.200 ; 0.466)
Res	1.653 (1.312 ; 2.156)	0.581 (0.440 ; 0.809)	0.485 (0.362 ; 0.642)	0.697 (0.524 ; 0.941)

All results are presented as coefficients (β) with 95% credible intervals (CrI). 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 of the female and Time TR the sum of the two latter traits. T of day = time of day, BM = body mass, and (a) and (w) represent the between- and within-individual components of the fixed effects, respectively.

[a] 'Spring' is used as references category

[b] '2011' is used as reference category

[c] "spontaneous enter" is used as reference category

491   **Table 3.** Adjusted repeatability estimates for the investigated traits across different time periods.

	V_I	V_R	R
Overall			
Expl (PC)[*$#]	0.882 (0.586 ; 1.261)	1.663 (1.296 ; 2.200)	0.34 (0.23 ; 0.47)
Time TR[*]	0.357 (0.175 ; 0.869)	0.604 (0.431 ; 0.907)	0.44 (0.24 ; 0.64)
Time NB[*$]	0.388 (0.182 ; 0.864)	0.506 (0.354 ; 0.766)	0.46 (0.26 ; 0.68)
Time FE	0.277 (0.131 ; 0.783)	0.747 (0.498 ; 1.058)	0.33 (0.15 ; 0.55)
Short-term			
Expl (PC)[#]	0.583 (0.347 ; 0.937)	1.170 (0.837 ; 1.742)	0.33 (0.20 ; 0.49)
Across-season			
Expl (PC)[*]	0.629 (0.171 ; 2.007)	1.784 (1.096 ; 3.036)	0.25 (0.09 ; 0.57)
Time TR[*]	0.351 (0.102 ; 0.942)	0.619 (0.362 ; 1.013)	0.41 (0.17 ; 0.66)
Time NB[*]	0.329 (0.104 ; 0.656)	0.500 (0.350 ; 0.917)	0.35 (0.15 ; 0.58)
Time FE	0.335 (0.121 ; 0.967)	0.755 (0.467 ; 1.195)	0.35 (0.13 ; 0.60)
Across-year			
Expl (PC)[$]	0.710 (0.153 ; 1.553)	1.572 (0.906 ; 2.351)	0.30 (0.10 ; 0.55)
Time TR	0.359 (0.111 ; 0.858)	0.851 (0.494 ; 1.282)	0.31 (0.12 ; 0.56)
Time NB[$]	0.301 (0.125 ; 0.759)	0.467 (0.306 ; 0.814)	0.41 (0.20 ; 0.64)
Time FE	0.393 (0.075 ; 0.797)	1.012 (0.626 ; 1.538)	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 ± 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.

[*] season was significant fixed effect
[$] year was significant fixed effect
[#] estimates from univariate mixed model presented (due to unbalanced experimental design)

492

493 **Table 4.** Between- and within-individual correlation between the investigated traits across different time
494 periods.

	Expl (PC)	Time TR	Time NB	Time FE
Overall				
Expl (PC)	-	-0.307 (-0.644 ; 0.372)	-0.200 (-0.600 ; 0.431)	0.294 (-0.441 ; 0.649)
Time TR	0.203 (-0.082 ; 0.418)	-	**0.573 (0.207 ; 0.853)**	**0.637 (0.176 ; 0.869)**
Time NB	0.199 (-0.070 ; 0.440)	**0.412 (0.199 ; 0.609)**	-	0.139 (-0.491 ; 0.585)
Time FE	0.107 (-0.101 ; 0.408)	**0.701 (0.550 ; 0.812)**	-0.163 (-0.386 ; 0.095)	-
Across-season				
Expl (PC)	-	0.100 (-0.695 ; 0.577)	-0.113 (-0.659 ; 0.530)	0.209 (-0.605 ; 0.682)
Time TR	0.015 (-0.292 ; 0.380)	-	**0.537 (0.029 ; 0.872)**	**0.827 (0.334 ; 0.918)**
Time NB	0.100 (-0.189 ; 0.422)	**0.452 (0.158 ; 0.704)**	-	0.138 (-0.458 ; 0.684)
Time FE	0.037 (-0.276 ; 0.395)	**0.752 (0.519 ; 0.861)**	-0.128 (-0.442 ; 0.214)	-
Across-year				
Expl (PC)	-	-0.263 (-0.748 ; 0.452)	-0.117 (-0.716 ; 0.408)	0.174 (-0.610 ; 0.669)
Time TR	0.317 (-0.079 ; 0.538)	-	0.519 (-0.077 ; 0.547)	**0.622 (0.087 ; 0.880)**
Time NB	0.379 (-0.007 ; 0.583)	**0.470 (0.159 ; 0.691)**	-	-0.147 (-0.632 ; 0.521)
Time FE	0.147 (-0.136 ; 0.475)	**0.808 (0.607 ; 0.873)**	-0.126 (-0.365 ; 0.239)	-

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 ± 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.

495

496   FIGURES

497   **Figure 1.** Schematic overview of the test room. The entrance hole in the test room was connected to the

498   start box attached at the outside of the room while the nest hole was connected to a nestbox attached at

499   the outside of the room (marked in grey). The wired mesh front wall is not depicted.

500   **Figure 2.** Exploration score (PC) per trial (mean± SE) for 30 male starlings. For inter-trial intervals see

501   Table 1.

502   **Figure 3.** Proportional times (mean ± SE) for the three sociability traits during the sociability assay over

503   the different trials for 30 male starlings. Time NB refers to the time spent near the nestbox and Time FE

504   to the time spent in proximity of the female. Time TR is the sum of Time NB and Time FE. For inter-

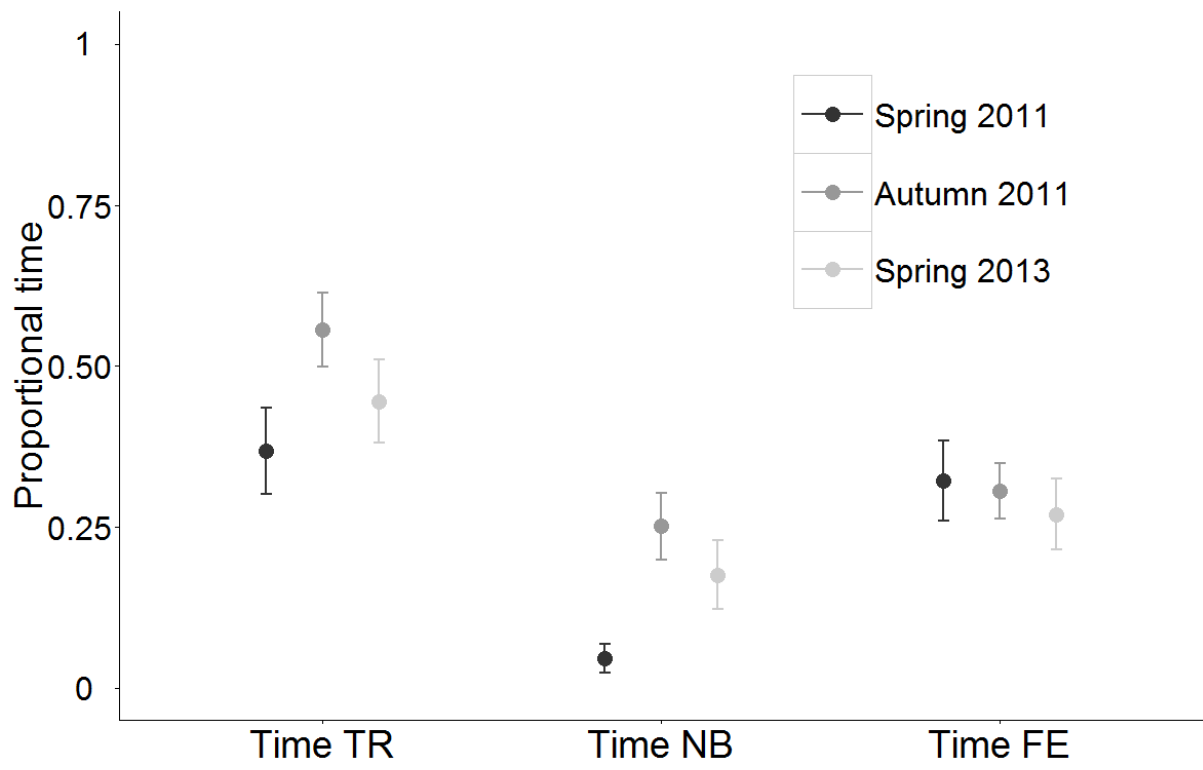505   trial intervals see Table 1.

506   Figure 1

507
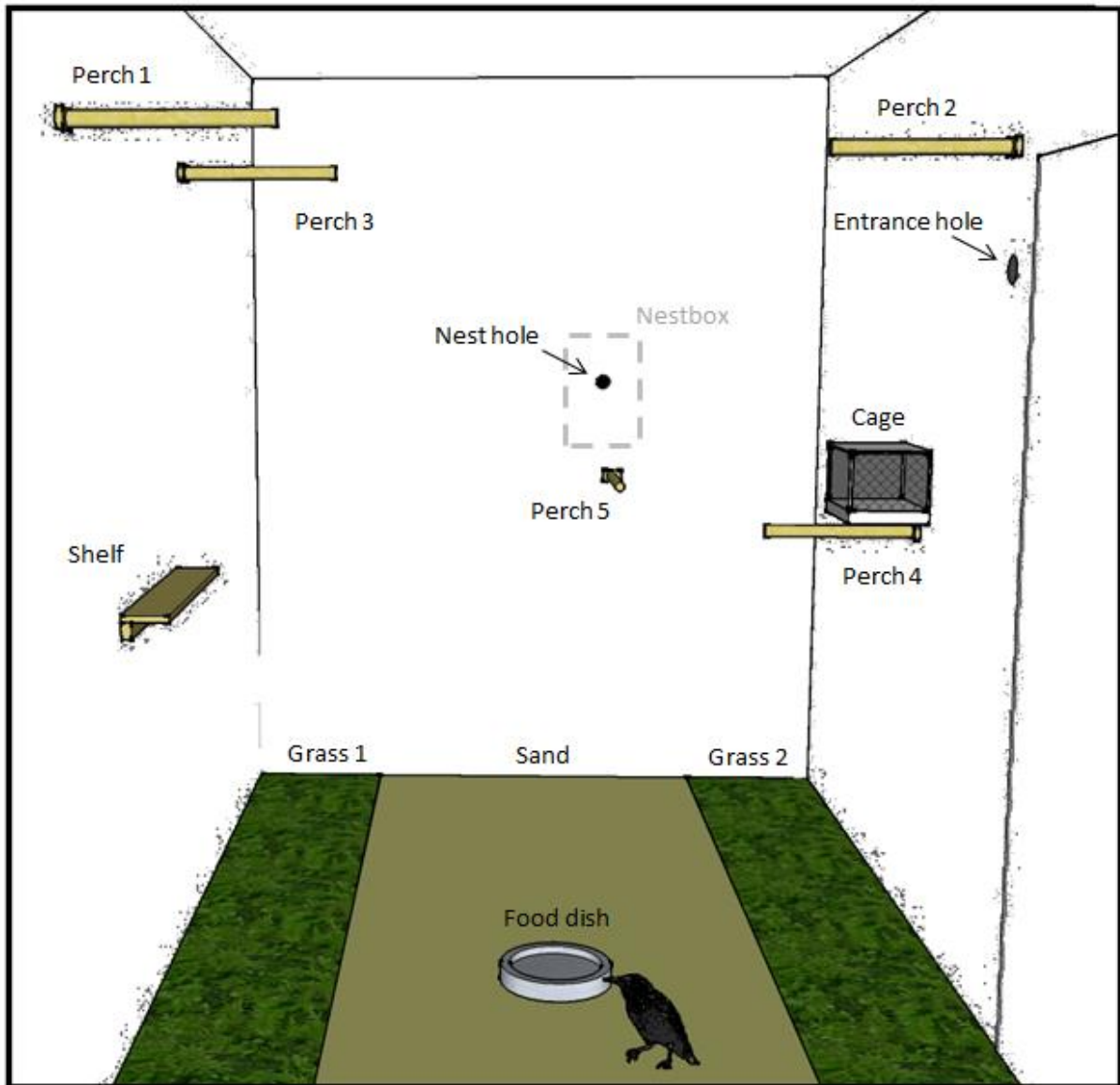
508　　　Figure 2
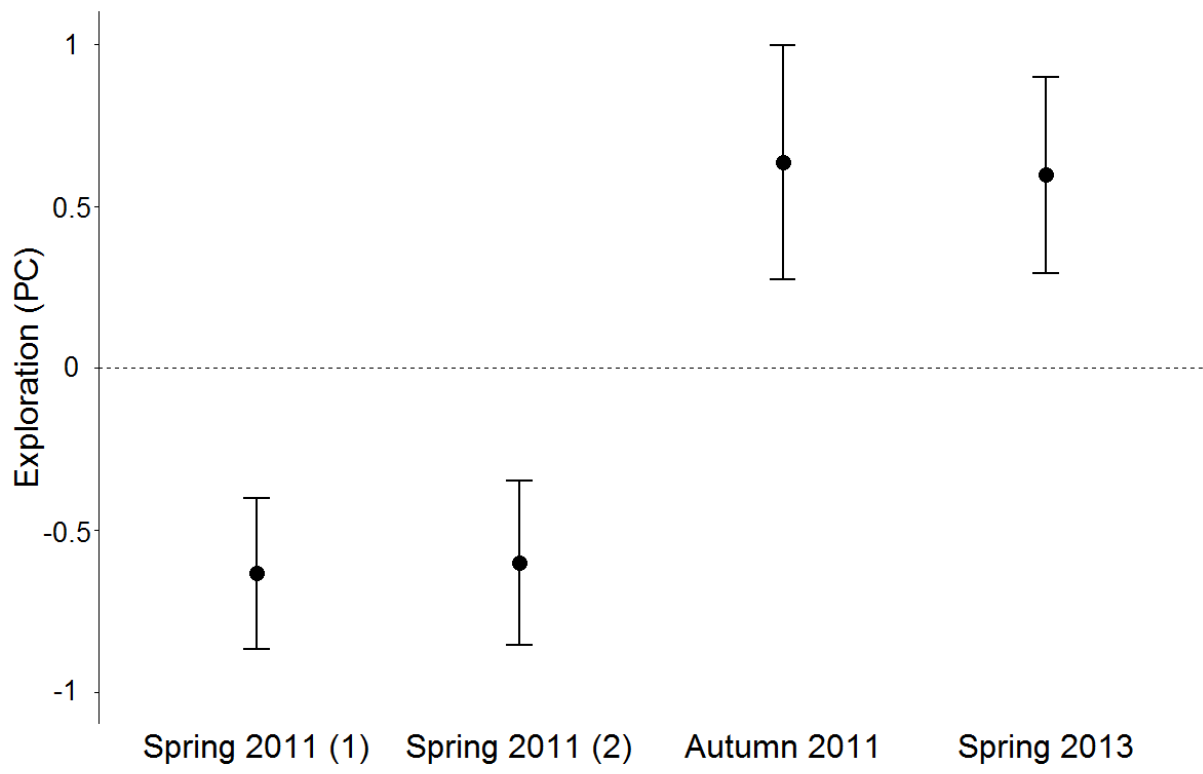
509

510   Figure 3

511

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