Behavioural syndrome between boldness and aggressiveness and link with reproductive success in a wild bird population

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27 **Abstract**

28 Boldness, defined as the behavioural response of individuals when facing a risky situation, is

29 a major personality trait and often phenotypically correlates with other behavioural traits, in

30 particular aggressiveness, exploration behaviour and neophobia. Yet, whether such links

31 result from among-individual correlations, i.e. form behavioural syndromes *stricto sensu*, is

32 often ignored and whether such syndromes may yield individual fitness benefits, and thus be

33 selected for, remains poorly explored. We measured boldness as the nest defence behaviour

34 against a dummy nest predator in a natural population of a small passerine bird, the collared

35 flycatcher, and investigated the existence of a behavioural syndrome between boldness and

36 two other behavioural traits, aggressiveness (measured as the agonistic response to

37 competitors) and neophobia (measured as the behavioural response to a novel object in a

38 known environment). Then we assessed the links between this potential syndrome and

39 reproductive success, measured as fledging and recruitment success. Boldness score differed

40 between sexes and depended on whether the partner was present during the test. Nevertheless,

41 it was repeatable, showing that boldness can be considered as a personality trait in our

42 population. We found a positive among-individual correlation between boldness and

43 aggressiveness, showing the existence of a behavioural syndrome between both personality

44 traits. This syndrome was related to reproductive success: the number of fledged young (but

45 not recruitment probability) increased with one integrative value of the boldness-

46 aggressiveness syndrome. Conversely, boldness score was not correlated to neophobia. Our

47 results thus clearly reveal a behavioural syndrome between boldness and aggressiveness with

48 possible consequences on reproductive success in the study population, and therefore open up

49 the question of the evolutionary implications of such a behavioural syndrome.

Introduction

Predation has long been recognized as a major evolutionary pressure shaping life-history strategies in the wild (e.g. in birds: Ricklefs, 1970; Oro et al., 1999; Martin & Briskie, 2009; in fish: Strauss, 1990; in arthropods: Caramujo et al., 1997). The behavioural response of individuals to predation threats has therefore received much attention. The propensity to take risks in a well-identified dangerous situation such as a predator attack defines boldness (Kleindorfer et al., 2005; Réale et al., 2007; Barnett et al., 2012). Due to the potential consequences of taking risks when defending oneself or one's young, boldness level can be expected to be under strong selective pressures (Traisnel & Pichegru, 2018; see also Dingemanse & Réale, 2005). Boldness has been found to positively associate with individual fitness components, such as survival (e.g. Richardson et al., 2019) and reproductive success, including mating success (e.g. Reaney & Backwell, 2007; Ward-Fear et al., 2018) and offspring number and/or condition (e.g. Bubac et al., 2018; Hollander, Van Overveld, Tokka, & Matthysen, 2008). Yet boldness also incurs costs, such as increased injury risk and individual mortality (Claireaux et al., 2018; Ward-Fear et al., 2018), and/or increased metabolic rate (Mathot, Dingemanse & Nakagawa, 2019) and daily energy expenditure (Careau, Thomas, Humphries & Réale, 2008). Thus selection should favour the adjustment of boldness level depending on its costs and benefits balance as a function of other phenotypic traits in given environmental conditions (Richardson et al., 2019). Understanding the consequences of the interplay between boldness and other phenotypic traits on fitness in the wild therefore represents a major research theme in behavioural ecology.

The interdependence of suites of phenotypic traits has been under recent focus in natural populations, in particular as a mechanism underlying the maintenance of among-individual behavioural differences that are consistent over time and contexts (i.e. repeatable),

75 defined as personality traits (Réale et al., 2007; Dall et al., 2004; Sih et al., 2004; Réale et al.,

76 2010; Wolf & Weissing, 2012), among which boldness. Many studies have indeed reported

77 boldness to be repeatable (Bell et al., 2009). The links now described over many taxa between

78 different personality traits and/or between personality and other phenotypic traits, e.g.

79 physiological and life history traits (Smith & Blumstein, 2008; Réale et al., 2010), have led to

80 the conceptualisation of main behavioural types along a proactive-reactive continuum (Øverli

81 et al., 2007; Toms et al., 2010; Castanheira et al., 2016). Accordingly, boldness has been

82 found to correlate positively with aggressiveness (measured as breeding site or territory

83 defence against competitors) and exploration behaviour (measured as the behavioural

84 response to a novel environment), and negatively with neophobia (measured as the response

85 to a novel object) (Sih & Bell, 2008; Kendall et al., 2018). In a (non-exhaustive) review of the

86 literature on the links between boldness and other behavioural traits, we found a total of 14

87 studies exploring these links: significant correlations with aggressiveness were reported in 9

88 studies out of 11, with exploration behaviour in 4 studies out of 5 and with neophobia in 2

89 studies out of 3 (Appendix Table A1). Such correlations can be modulated by environmental

90 factors (e.g. degree of urbanization: Myers & Hyman, 2016; Ducatez et al., 2017). If boldness

91 positively correlates with aggressiveness and exploration, bold individuals may be more

92 competitive and occupy larger and/or higher quality territories compared to shy ones (e.g.

93 Ward-Fear et al., 2018), as well as locate and access food more quickly (Kurvers et al., 2009,

94 2012; Dammhahn & Almeling, 2012). Consequently, boldness may be associated with fitness

95 benefits through increased foraging success (Short & Petren, 2008; Patrick & Weimerskirch,

96 2014; Richardson et al., 2019) as a result from links with other personality traits, outside a

97 risk context. Links with other traits can thus constrain or facilitate the response of boldness to

98 evolutionary pressures.

99   However, the evolutionary consequences of a phenotypic correlation between traits

100   will depend on whether this correlation results from among-individual rather than common-

101   environment and/or within-individual (or residual) correlation (Sih et al., 2004), i.e. if it

102   represents a behavioural syndrome *stricto sensu* (Dingemanse et al., 2010; Dingemanse &

103   Réale, 2013; Brommer, 2013; Niemelä & Dingemanse, 2018). Very few studies (3 out of the

104   14 reviewed, to our knowledge; Appendix Table A1) actually explored whether the observed

105   phenotypic correlations between boldness and other traits resulted from among-individual

106   correlations. This was the case in only one study, showing a behavioural syndrome with

107   aggressiveness (Garamszegi et al., 2015). Furthermore, the functional integration of a

108   combination of phenotypic traits, resulting in a behavioural syndrome, will occur only if this

109   syndrome increases fitness, at least in given environmental conditions (Dingemanse et al.,

110   2007). Even though boldness is often found to be linked with measures of individual fitness (8

111   out of 9 studies in our review: Appendix, Table A1; Smith & Blumstein, 2008), no study to

112   our knowledge investigated the links between syndromes involving boldness and fitness

113   measures (Dingemanse & Réale, 2005, Wolf & Weissing, 2012; but see Bell & Sih, 2007 for

114   a case based on phenotypic correlations). Assessing the fitness consequences of such

115   syndromes thus remains an open question.

116   In this study, we explored variation in boldness level, measured *in natura* as the nest

117   defence behaviour towards a nest predator, in a breeding population of a small passerine bird,

118   the collared flycatcher *Ficedula albicollis*. In particular, we investigated whether boldness

119   forms a behavioural syndrome with two other behavioural traits, aggressiveness and

120   neophobia, and whether this potential syndrome relates to reproductive success. We first

121   assessed within and between-year repeatability and sources of variation in boldness level

122   against nest predators (including heritability). Previous studies in this species found that

123   boldness measured as the behavioural response towards human presence, as well as

124 aggressiveness and neophobia, were repeatable between years, i.e. can be considered as

125 personality traits (Garamszegi et al., 2009, 2016; Morinay et al., 2019). We therefore expected

126 our boldness score to also reflect a personality trait. Second, we explored the among- and

127 within-individual correlation between boldness and aggressiveness (measured as the agonistic

128 behavioural response towards competitors), and between boldness and neophobia (measured

129 as the response to the presence of a novel object near the nest). Based on results from a meta-

130 analysis (Sih & Bell, 2008; see also Appendix Table A1), we expected phenotypic

131 correlations between these traits, but explored here specifically whether such correlations

132 reflected a behavioural syndrome. Finally, we tested whether a potential syndrome involving

133 boldness was related to reproductive success, measured here by the number of fledged young

134 and recruitment probability, and could thus be under selection. The maintenance of a

135 syndrome can indeed be expected to result from increased fitness benefits of the combination

136 of traits compared to each trait taken independently.

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138

139 **Materials and methods**

140

141 *Study site, study species and population monitoring*

142   Data were collected in a natural population of a small migratory, cavity-nesting

143 passerine bird, the collared flycatcher, breeding on the island of Gotland (Southern Baltic Sea,

144 Sweden; 57°03'N, 18°18'E). Flycatchers arrive on the breeding grounds from late April until

145 late May. Because of strong time constraints, females lay only one clutch, between mid-May

146 and early June (except for rare replacement clutches by pairs that failed very early). In the

147 study area, several hundreds of flycatcher pairs readily breed each year in 1800 nestboxes

148 provided in excess in 20 woodland patches of 2 to 25 ha separated by unsuitable habitat (i.e.

149   pastures, fields). Since 1980, nestboxes have been regularly visited (at least once a week) each

150   year from May to July to record main breeding data, including laying and hatching dates,

151   clutch size, nestling number and condition and final fledging success. On average, 1/3 of nests

152   fail every year before fledging (between 25 and 50% depending on environmental conditions).

153   Adults breeding in nestboxes have been captured for identification, aging (based on plumage

154   characteristics; Svensson, 1992) and measuring (as well as ringing if previously unringed),

155   during incubation for females and nestling rearing for males. Part of the males are

156   polygynous, providing little care to the young of the secondary female, which often leads to

157   brood failure and the impossibility to catch the male (Gustafsson, 1989). Nestlings were

158   ringed 7 to 12 days posthatching (fledging usually occurs around day 16 posthatching). For

159   more information on the study site and long-term population monitoring, see Pärt &

160   Gustafsson (1989), Doligez et al. (1999, 2004, 2009).

161

162   *Aggressiveness, neophobia and boldness tests*

163   From 2011 to 2014, three separate behavioural tests were implemented *in natura* on as

164   many pairs as possible in the population, to score the following traits (Réale et al., 2007), in

165   chronological order (Fig. 1): (1) aggressiveness, measured as the agonistic response to a

166   simulated territorial intrusion by intra- or interspecific competitors during the nest building

167   stage; (2) neophobia, measured as the latency to resume nestling feeding in the presence of a

168   novel object on the nestbox during the early nestling stage (i.e. day 5-6 posthatching), and (3)

169   boldness, measured as the risk-taking response to a simulated attack by a nest predator during

170   the late nestling stage (i.e. day 13-14 posthatching). These three tests were thus conducted in

171   different contexts, corresponding to different personality traits: behavioural response in a

172   social context with no or small deadly risk (aggressiveness), response to novelty in a known

173   environment with unknown risk (neophobia) and response to a dangerous situation with

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174 known deadly risk (boldness; see Réale et al., 2007, for trait definition). Flycatchers show

175 plumage colour dimorphism allowing an easy distinction between males and females from a

176 distance during behavioural tests.

177   To measure aggressiveness, we simulated intrusion by a competitor at the time when

178 the risk of losing the box is maximal in this single-clutch species with decoys of either a

179 collared flycatcher pair (intraspecific competitors) or a single great tit (interspecific

180 competitor for nestboxes; Gustafsson, 1987; Forsman et al., 2014). The observer first placed

181 the decoy(s) on the nestbox and then recorded (while hidden) the following behavioural

182 responses by each focal parent: (i) the presence of the bird within four a priori defined

183 distance categories from the nestbox (< 2 m, 2 to 5 m, 5 to 10 m, > 10 m) and all movements

184 within and between these distance categories, (ii) agonistic behaviours towards the stimulus,

185 including attacks and stationary flights in front of the decoy(s), and (iii) chases towards live

186 birds attracted around the nestbox by the stimulus. Recording started immediately after the

187 observer has hidden and continued uninterrupted until the end of the test, whether the bird left

188 the surroundings or not during the test. Tests were performed two to four times depending on

189 field constraints, alternating both stimuli (intra- vs. interspecific), at one day intervals (with

190 one day free from tests in between two series of two tests). For each test, we calculated a

191 behavioural response score following Morinay et al. (2019) by summing the number of (i)

192 movements within the closest zone (i.e. < 2 m) to the nestbox, (ii) agonistic behaviours and

193 (iii) chases, and dividing this sum by the time interval between the first observation of the

194 individual and the end of the test, rescaled to 15 min. For more details, see Fig. 1 and Morinay

195 et al. (2019).

196   The neophobia test consisted in two consecutive 1-hour long periods during which the

197 behaviour of parents at the nest was video recorded first in the absence of any source of

198 disturbance other than the video recorder (first 1h-period) and second in presence of a novel

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199   object (a coloured plastic figurine) placed just beside the nestbox entrance (second 1h-period).

200   This allowed us to compare the time needed to resume nestling feeding with and without the

201   novel object while controlling for human disturbance at the nest and other factors potentially

202   affecting provisioning behaviour such as nestling hunger level. We calculated the neophobia

203   score of each parent as the ratio of the latency (time in s) to resume nestling feeding in

204   presence of the novel object (second period of the test) over the latency to resume feeding in

205   absence of the novel object (first period). To include the individuals that never resumed

206   feeding in presence of the novel object, i.e. the most neophobic ones, we assigned them the

207   maximal latency observed over all tests (i.e. 4000 s here because tests may sometimes last

208   longer than 1 h due to logistical constraints in the field). We excluded from the analyses the

209   few individuals (74 of 1334 observations, i.e. 5.5%) that did not resume feeding without the

210   novel object (first part of the test) because they may have been disturbed by the video

211   recorder. In most cases, both parents returned quickly to the nestbox in the first part of the test

212   (median time of return: 6 min 44 s). For more details, see Fig. 1 and Morinay et al. (2019).

213   To measure boldness, we simulated an attack by a nest predator to elicit nest defence

214   in response to the risk of losing the brood with a dummy of a red squirrel or great spotted

215   woodpecker (in 2011 only). These predators have been found to occasionally attack flycatcher

216   broods but also parents, and they are often alarmed at and chased by parents when close to the

217   nestbox (Doligez & Clobert, 2003). They represent the main potential nest predators on

218   Gotland where mustelids are absent. The observer first placed the dummy nest predator on the

219   box and then recorded (while hidden) the same behavioural responses of each focal parent

220   than in the aggressiveness test. Again, recording started immediately after the observer was

221   hidden and continued uninterrupted until the end of the test. Tests were performed once or

222   twice on consecutive days depending on field constraints. For each test, we calculated a

223   behavioural response score following Tamin & Doligez (2022) by summing the number of

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224 movements within the closest zone (i.e. < 2 m) to the nestbox and attack behaviours

225 (excluding chases), and dividing this sum by the time interval between the first observation of

226 the individual and the end of the test, rescaled to 5 min. We checked whether our results were

227 robust to this boldness score by repeating the analyses using the first principal component of a

228 PCA based on the different behavioural responses recorded during the test as an alternative

229 score (see Appendix and Récapet et al., 2016). For more details, see Fig. 1 and Récapet et al.

230 (2016), Tamin & Doligez (2022).

231 A previous study in this population quantified a boldness response to human presence

232 at the nestbox (i.e. another potentially dangerous situation associated with known deadly risk)

233 as the latency to return to the nest and resume nestling feeding after a human visit, during the

234 first part of the neophobia test (Morinay et al., 2019). The level of repeatability of this

235 boldness score was however low ($R = 0.11$, 95% CI = [0.01; 0.21]) compared to repeatability

236 usually reported for anti-predator behaviours (on average 0.40; Bell et al., 2009). Using the

237 latency to return to the nest as a score in our nest predator boldness test also yielded a low

238 repeatability level ($R = 0.07$, 95% CI = [0.02; 0.13]) compared to the score described above

239 (see Results). Finally, both latencies were not correlated (Pearson correlation: -0.03 [-0.10;

240 0.04]). Because the neophobia test was not initially intended to measure boldness in our case

241 and because the risk-taking response in this context may be questioned (individuals actually

242 return after the risk has ended), we thus choose not to use latency here as a boldness score and

243 did not test the link between our boldness score and the score previously described (Morinay

244 et al., 2019; see also Discussion). Including the latency to resume feeding in the first period of

245 the test in the direct computation of our neophobia score also prevented us to use it as a

246 boldness measure here. The total and yearly numbers of individuals tested for each trait is

247 given in Table A2.

248

Ethical Note

250   Permission for catching and ringing adults and nestlings (approximatively 4000

251 individuals between 2011 and 2014) with individually numbered aluminium rings was granted

252 every year by the Ringing Centre of the Museum of Natural History in Stockholm (licence nb.

253 471:M015 to B.D.). Adult catching and nestling ringing were performed following the

254 methods described in Morinay et al., 2019. During the aggressiveness and boldness tests, we

255 minimized disturbance by approaching the nestbox as quietly as possible and hiding below a

256 camouflage net far away enough not to be detected by individuals. For the neophobia test, we

257 controlled nestling satiety both at the beginning and in between the two parts of the test, and

258 we cancelled the test if nestlings were begging too strongly to avoid potential negative impact

259 of a temporary decrease in parental provisioning due to the presence of the novel object. All

260 the manipulations were performed in accordance with the Swedish legislation applying at the

261 time.

262

263 *Statistical analyses*

264 Sources of variation in boldness score: univariate GLMMs

265   We assessed among- and within-individual sources of variation in boldness using a

266 univariate generalized linear mixed model with boldness score as the response variable. The

267 model included as fixed effects individual sex and age (two categories: yearling *vs.* older

268 individual), test order (first or second test for the focal individual, in the cases when two tests

269 were performed in the same year), test date and its squared value (to test for quadratic

270 temporal trends due to differences in the cost/benefit balance of nest defence along the

271 season) and the presence of the partner during the test (which may influence the focal

272 individual's behaviour; Morinay et al., 2019 - see Table A3 for the spelling out of models).

273 Including clutch size as a measure of reproductive investment (previously shown to affect

274   boldness level) or replacing test date by laying date did not change the results (level of

275   repeatability or estimates of other effects, not detailed here). Similarly, including the number

276   of tests the individual has been subjected to in previous years as a measure of its past

277   experience imposed by the test design did not change the results, even though boldness score

278   tended to increase with the number of tests the individual had been subjected to (posterior

279   mode [95% CI]: 0.18 [-0.0003; 0.34]). The model also included as random effects individual

280   identity, observer, dummy identity and the combination of year and woodland patch (to model

281   spatio-temporal environmental variation). We combined patch and year effects here because

282   we were not interested in characterizing spatial and temporal variations separately and to ease

283   model convergence; including them as separate random effects did however not change the

284   results (not detailed here). We obtained 2101 values of boldness score over all tests, with 1.34

285   tests per individual on average in a given year. We calculated within-year repeatability of

286   boldness score (R) as the individual identity variance ($V_{individual}$) divided by the total

287   phenotypic variance (V_P, sum of all variances; Falconer & Mackay, 1996). Because not all

288   individuals were of known pedigree, we estimated the heritability of boldness using a separate

289   model including the same fixed effects and as random effects the additive genetic effect

290   (associated with the pedigree), maternal and paternal identities, permanent environmental

291   effect (from individual identity once genetic and parental effects have been accounted for),

292   observer, dummy identity and the combination of year and woodland patch. We obtained 671

293   values of boldness score over all tests with full pedigree information and we calculated

294   boldness score heritability (h^2) as the additive genetic variance (V_A) divided by the total

295   phenotypic variance (V_P; Falconer & Mackay, 1996).

296   Part of the individuals were measured in several years, thus we also calculated

297   between-year repeatability using another model, with the average value of boldness score over

298   the different tests for a given individual in a given year as the response variable; the model

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299 included again sex, age, average test date and its squared value as fixed effects, as well as

300 individual identity and combination of year and patch as random effects (but no additive

301 genetic effect here). We obtained in this case 1384 averaged values of boldness score, with

302 1.13 tests per individual on average over all years. We calculated between-year repeatability

303 of boldness score (R) as the individual identity variance ($V_{individual}$) divided by the total

304 phenotypic variance (V_P). Although both within- and between-year repeatability could in

305 theory be estimated in a single model by including individual identity and the combination of

306 individual identity with year simultaneously as random effects (Araya-Ajoy et al., 2015), the

307 number of within- and between-year repetitions of boldness scores per individual was too low

308 here to yield a robust model. Thus two separate models had to be used even though this may

309 yield less precise repeatability estimates. Because repeatability estimates may be affected by

310 the presence of fixed factors in the model (Nakagawa & Schielzeth, 2010), we also compared

311 repeatability obtained for the two models (within- and between-year) both with and without

312 fixed effects by checking whether the 95% CI overlapped.

313

314 Behavioural syndromes: PCA and bivariate GLMMs

315   We investigated possible behavioural syndromes between boldness and the two other

316 behavioural traits, aggressiveness and neophobia. These two traits have been found to be

317 repeatable (Morinay et al., 2019; between-year repeatability here based on the slightly

318 modified data set including 2014 data: aggressiveness: $N = 1291$ individuals, $R = 0.26$, 95%

319 CI = [0.11; 0.38]; neophobia: $N = 852$ individuals, $R = 0.31$, 95% CI = [0.15; 0.48]). We first

320 explored the correlations between the three traits using a principal component analysis on the

321 aggressiveness, boldness and neophobia scores (Cote et al., 2010a). Aggressiveness and

322 boldness scores were averaged over the different tests to obtain a single value for a given

323 individual in a given year; averaging score values is expected to decrease the influence of

13

324 external factors on behavioural scores (see Morinay et al., 2019). We did not differentiate

325 aggressiveness in response to intra- and inter-specific competition because aggressiveness

326 score did not depend on stimulus type (Morinay et al., 2019). We obtained 688 observations

327 of individuals with a score for the three behavioural traits simultaneously. We used varimax

328 rotation (Quinn & Keough, 2002) and identified principal components with the scree plot and

329 a bootstrapped Kaiser-Guttman (Jackson, 1993); behavioural traits were considered to

330 contribute to principal components when their loading was above 0.32 (Tabachnick & Fidell,

331 1996).

332   Second, we used bivariate generalised linear mixed models to partition the phenotypic

333 correlation between boldness and the two other personality traits into among-individual,

334 environmental and within-individual (residual) correlations. We did not implement a single

335 trivariate model on the three traits because this would drastically reduce our sample sizes

336 (40.7% of observations for the boldness and aggressiveness model would be excluded due to

337 missing neophobia score and 15.8% for the boldness and neophobia model due to missing

338 aggressiveness score). Furthermore, the correlation between aggressiveness and neophobia

339 has already been assessed (Morinay et al., 2019). As above, the two bivariate models

340 (boldness-aggressiveness and boldness-neophobia) used average score values (when repeated

341 tests were conducted on the same individual for a given trait in a given year) and included as

342 fixed traits sex, age, average test date and average test date^2 for each trait to account here for

343 possible temporal trends; they also included as random effects individual identity and the

344 combination of year and patch. We did not include an additive genetic effect since none of the

345 three traits were found to be heritable (Morinay et al., 2019 and results below for boldness).

346 Here again, including clutch size or year and patch as separate random effects did not change

347 the results (not detailed here). We obtained 979 observations of individuals with both

348 boldness and aggressiveness scores and 694 with both boldness and neophobia scores. The

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349   phenotypic correlation between two behavioural traits A and B, $r_{PA,PB}$, and the among-

350   individual correlation between A and B, $r_{indA,indB}$, were estimated as follows from variances

351   and covariances estimated by the models (Snijders & Bosker, 1999):

352
$$r_{PA,PB} = \frac{Cov_{indA,indB} + Cov_{envA,envB} + Cov_{\varepsilon A,\varepsilon B}}{\sqrt{(V_{PA} \times V_{PB})}}$$

353
$$r_{indA,indB} = \frac{Cov_{indA,indB}}{\sqrt{(V_{indA} \times V_{indB})}}$$

354   where $Cov_{indA,indB}$, $Cov_{envA,envB}$ and $Cov_{\varepsilon A,\varepsilon B}$ are respectively the among-individual (i.e.

355   individual identity), environmental (i.e. the combination of year and patch) and within-

356   individual (i.e. residual) covariances between traits A and B, and V_{PA} and V_{PB} the total

357   phenotypic variance for traits A and B respectively (sum of the among-individual, common-

358   environment and within-individual variances).

359

360   <u>Link between syndrome and reproductive success: univariate GLMMs</u>

361   To investigate the possible link between reproductive success and a behavioural

362   syndrome involving the traits considered, we first used the value of the first principal

363   component of the PCA on the three traits as an integrative behavioural syndrome score (Cote

364   et al., 2010a; Budaev, 2010; McEvoy et al., 2015). We tested whether this first principal

365   component was linked to the number of fledged young and their local recruitment probability

366   in the following year(s) (i.e. including the juvenile survival phase) using two univariate mixed

367   models. The response variables were either the number of fledged young (from 0 to 8) or local

368   recruitment success (0 if none of the fledged young recruited in the local population, i.e. was

369   captured as an adult, in the following two years or 1 if at least one young recruited; in the

370   sample used here, 105 nests over 380, i.e. 27.6 %, produced at least one recruit). The models

371   included as fixed effects the first principal component, its square value, sex, age, laying date

372   and laying date² (to account for the seasonal decrease in reproductive success previously

373   reported in this population: Wiggins et al., 1994), as well as individual identity and the

374   combination of year and patch as random effects. We added the square value of the first

375   principal component to investigate a possible non-linear synergetic effect of the combination

376   of traits involved in a syndrome. Higher relative reproductive benefits could indeed be

377   expected for individuals showing either high or low values of several traits simultaneously,

378   leading to a potential functional integration of these traits.

379   Because the first principal component of the PCA however explained only part of the

380   between-individual variation in behavioural scores, we also directly investigated the links

381   between reproductive success measures and the behavioural traits involved in the identified

382   syndrome(s) (i.e. with loading > 0.32 on the first principal component) and their interaction as

383   an alternative measure of the syndrome(s). We thus tested whether the interaction between

384   trait scores was linked to the number of fledged young and their local recruitment probability

385   using two new univariate mixed models with the same response variables and fixed and

386   random effects as above, except for the measure of the behavioural syndrome. In addition, we

387   tested whether these trait scores were independently linked to the same measures of

388   reproductive success by including them separately (thus with no interaction) in new univariate

389   models.

390   Importantly, we did not separate here successful from failed individuals (i.e. based on

391   whether at least one young fledged), as often done to account for a zero-inflated distribution

392   of the number of fledglings, because in our case, nearly all individuals in the sample were

393   successful (i.e. fledged at least one young: 381 out of 385, i.e. 99%). Indeed, the boldness test

394   was performed on pairs that reached the late nestling rearing stage. This automatically

395   excluded most failed pairs from testing both the existence of a behavioural syndrome between

396   boldness and other traits and the link between such a syndrome and reproductive success (see

397   Discussion for potential implications). The number of fledged young was thus normally

398 distributed in this biased sample. Because both parents within a pair shared the same number

399 of fledged and recruited young, we randomly selected the score of one pair member when we

400 had scores for both, to avoid the artificial inflation of reproductive success data due to

401 repeated values within pairs. The random selection was then repeated 100 times to assess the

402 robustness of the links between the measures of behavioural syndrome(s) and reproductive

403 success.

404

405 <u>Bayesian procedures</u>

406 We implemented our analyses within the Bayesian framework in R v3.6.3. Univariate

407 and bivariate (generalised) linear mixed models were run using the MCMCglmm function of

408 the *mcmcglmm* package (Hadfield, 2010) and fitted with a Poisson family (logit link) for

409 aggressiveness, neophobia and boldness scores, a Gaussian family for the number of fledged

410 young and a threshold family (here a binomial family, logit link) for the probability of

411 recruitment. In bivariate models, different test dates were fitted for each response variable

412 using the at.level() function. We implemented the randomisation procedure using the lapply

413 and mclapply functions of the *parallel* package (R Core team, 2022), which provide estimates

414 based on all randomisations combined, thus integrating the uncertainty on the randomly

415 selected data. In all models, we adjusted the number of iterations, burn-in and thinning

416 interval in order to achieve an effective sample size over 2000 and an autocorrelation level of

417 posterior samples below 0.1 in all cases. We used inverse Wishart and expanded priors for all

418 models for both fixed and random effects (univariate models: $V = 1$, $\nu = 1$, $\alpha\mu = 0$, $\alpha V = $

419 1000; bivariate models: $V = \text{diag}(2)$, $\nu = 2$, $\alpha\mu = c(0,0)$, $\alpha V = \text{diag}(2)$). We used the Gelman

420 and Rubin approach to assess the convergence of each of three MCMC chains per model

421 (gelman.diag and gelman.plot functions, 'coda' R package; Plummer, Best, Cowles & Vines,

422   2006). All estimates are presented as posterior modes with associated 95% credible intervals

423   (CI) unless otherwise stated.

424

425

426   **Results**

427

428   *Sources of variance in boldness score*

429   Boldness score was repeatable both within- and between years, with no major

430   difference when fixed effects were included or not (estimates [95% CI] with *vs.* without fixed

431   effects: within-year: $N = 1228$ individuals, $R = 0.39$ [0.31; 0.46] *vs.* $N = 1228$ individuals, $R =$

432   0.40 [0.33; 0.47]; between-years: $N = 1204$ individuals, $R = 0.43$ [0.31; 0.58] *vs.* $N = 1204$

433   individuals, $R = 0.49$ [0.32; 0.58]). Using the first principal component of the PCA on all

434   behaviours recorded during the test as an alternative boldness score yielded similar results

435   even though repeatability levels were lower (Appendix Table A4). Boldness was not heritable

436   (h^2 estimate [95% CI] = 0.00 [0.00; 0.20] with fixed effects; 0.00 [0.00; 0.18] without fixed

437   effects; repeatability estimates did not decrease when additive genetic and parental effects

438   were included: Table A5).

439   Boldness score was higher for males compared to females, as well as when the partner

440   was present during the test compared to when the individual was alone (Table 1). It was also

441   higher in the second test compared to the first when two tests were performed for a given

442   individual in a given year (Table 1). Conversely, boldness score did not depend on age

443   category or test date (Table 1). Again, using the first principal component as an alternative

444   boldness score yielded similar results, except for test date and squared test date, with a score

445   first increasing and then decreasing with test date in this case (Appendix Table A4).

446

18

447 *Correlations between boldness, aggressiveness and neophobia scores*

448   In the PCA exploring the correlations between the three behavioural scores, we

449 identified two principal components explaining 75 % of the total variance (Table 2). The first

450 principal component showed high positive loadings (> 0.75) for both boldness and

451 aggressiveness scores while the second principal component showed a high loading (0.95) for

452 the neophobia score alone (Table 2). Thus boldness and aggressiveness scores appeared

453 strongly positively related and independent from the neophobia score.

454   The bivariate models confirmed this pattern: we observed a positive phenotypic

455 correlation between boldness and aggressiveness scores: more aggressive birds were also

456 bolder (Table 3). This phenotypic correlation resulted from a positive among-individual

457 correlation, while environmental and within-individual correlations did not differ from zero

458 (Table 3). Conversely, boldness and neophobia scores were not phenotypically correlated

459 (Table 3). Thus, boldness and aggressiveness, but not neophobia, form a behavioural

460 syndrome *stricto sensu*. Similar results were obtained when using the first principal

461 component as an alternative boldness score (Appendix Table A6).

462

463 *Relations between the boldness-aggressiveness syndrome and measures of reproductive*

464 *success*

465   The first principal component of the PCA between the three behavioural scores used

466 as a measure of the boldness-aggressiveness syndrome was repeatable between years ($N =$

467 583 individuals: $R = 0.39$, 95% CI = [0.04; 0.56]). The number of fledged young increased

468 with the first principal component over the randomisations with one individual per pair

469 randomly selected (posterior mode [95% CI]: 0.30 [0.05; 0.57]; Fig. 2a). Individuals that were

470 simultaneously more aggressive and bolder had a higher fledging success than less aggressive

471 and shyer ones (Fig. 3). The squared value of the first component had no effect on the number

of fledged young (posterior mode [95% CI]: -0.05 [-0.15; 0.02]; Fig. 2a). When directly

modelling the syndrome with the interaction between aggressiveness and boldness, the

number of fledged young was not related to the interaction (posterior mode [95% CI]:

6.33×10^{-5} [-3.28×10^{-4}; 4.58×10^{-4}]; Fig. 2b). In addition, the number of fledged young was

linked to neither aggressiveness nor boldness when included separately as fixed effects

(posterior mode [95% CI] for aggressiveness: 0.007 [-0.002; 0.015], for boldness: 0.007 [-

0.001; 0.015]). None of the other fixed effects were related to the number of fledged young

(Appendix Table A7).

The probability of recruitment was related to neither the first principal component

(posterior mode [95% CI]: 0.02 [-0.69; 0.77]) nor its squared value (posterior mode [95% CI]:

-0.06 [-0.47; 0.21]) over randomisations (Fig. 2a). When directly modelling the syndrome

with the interaction between aggressiveness and boldness, the probability of recruitment was

not related to the interaction (posterior mode [95% CI]: -0.0003 [-0.002; 0.001]; Fig. 2b); it

was not related to aggressiveness or boldness when included separately either (posterior mode

[95% CI]: for aggressiveness: -0.003 [-0.03; 0.02], for boldness: -0.003 [-0.03; 0.02]). Again,

none of the other fixed effects were related to the probability of recruitment (Appendix Table

A7).

Discussion

Boldness is a crucial trait shaping responses to risky situations. Yet, the fitness

consequences of the frequently observed relations between boldness and other traits remain

poorly explored in empirical studies. In a natural population of collared flycatchers, we

investigated (i) the sources of variation in boldness measured as nest defence behaviour

497   against a nest predator, (ii) whether boldness is correlated to two other personality traits

498   (aggressiveness and neophobia), forming a behavioural syndrome and (iii) to what extent this

499   syndrome is related to reproductive success, measured here as the number of fledged young

500   and recruitment probability. Besides variation due to individual and environmental factors

501   (sex, presence of the partner during the test), we found that boldness level was repeatable over

502   time both in the short- (within year) and long-term (between years), confirming results of

503   previous studies in many taxa (Réale et al., 2007; Bell et al., 2009) but it was not heritable. A

504   phenotypic correlation was observed between boldness and aggressiveness (but not

505   neophobia) and this correlation resulted from among-individual correlation, revealing a

506   boldness-aggressiveness behavioural syndrome in this population. This boldness-

507   aggressiveness syndrome was linked to our short-term measure of reproductive success, with

508   an increasing number of fledged young when the level of the boldness-aggressiveness

509   syndrome increased, but only when the syndrome was measured by the first principal

510   component of the PCA between the three traits. The syndrome showed no relation with future

511   recruitment probability. Our results may thus suggest fitness consequences of the observed

512   behavioural syndrome, but the resulting constraints on the joint evolution of the traits

513   concerned remain unclear, especially because none of the traits was heritable.

514

515   *Sources of variation in boldness and behavioural syndrome with aggressiveness*

516   Boldness, measured here as risk-taking behaviour in the context of nest defence, was

517   repeatable over time with a repeatability level similar to those previously reported (Bell et al.,

518   2009). It can thus be considered as a personality trait as in many other populations (e.g.

519   Duckworth, 2006; Kontiainen et al., 2009; Brommer et al., 2014; Fresneau et al., 2014;

520   Garamszegi et al., 2015; Traisnel & Pichegru, 2018). Interestingly, the study population is

521   exposed to a low nest predation pressure due to the absence of mustelids on Gotland. The

522   higher boldness level observed when the partner was present during the test could reflect

523   either (i) a flexible adjustment of risk-taking behaviour depending on the partner's behaviour

524   within a pair or (ii) assortative mating based on boldness. The partner's presence during the

525   test is indeed likely related to its own boldness level, since bolder individuals are more likely

526   to respond to the stimulus and thus be present. In turn, the partner could itself also be more

527   likely to be attracted by a higher nest defence response of the focal individual. Assortative

528   mating with respect to boldness has indeed been reported in different species (e.g. Kortet et

529   al., 2012; Ariyomo & Watt, 2013; Rabdeau et al., 2021) including our study population

530   (Tamin & Doligez, 2022).

531   Boldness score was here phenotypically positively correlated with aggressiveness

532   score, as previously described in different species (Appendix Table A1). Importantly, this

533   phenotypic correlation resulted from among-individual rather than within-individual

534   (residual) or environmental correlation (here, the year-patch combination). It thus constitutes

535   a behavioural syndrome *stricto sensu* (Dingemanse et al., 2010; Dingemanse & Réale, 2013;

536   Brommer, 2013) between boldness and aggressiveness, which could have potential

537   consequences for the joint evolution of both traits and their fitness consequences

538   (Dingemanse et al., 2004; Sih et al., 2004; Cote et al., 2010b; Karlsson Green et al., 2015).

539   Yet, none of the two traits were heritable (our results and Morinay et al., 2019). Such absence

540   of heritability could result in no constrained evolution for both traits despite the behavioural

541   syndrome described here. In the absence of genetic determinism for the two traits involved,

542   this syndrome could result from early growth conditions shaping the development of

543   behavioural type, which would deserve further investigation. More work is also needed to

544   explore the genetic and non-genetic inheritance of the syndromes themselves and how it may

545   shape their evolution, a question unexplored thus far.

546   Our results confirm the boldness-aggressiveness syndrome described for collared

547   flycatcher males in another population (Garamszegi et al., 2009, 2016) but they differ from

548   previous results obtained in the same population, with boldness measured in response to

549   human presence (Morinay et al., 2019). Aggressiveness was not correlated (and thus formed

550   no syndrome) with the latency to return to the nest after a visit by a human observer (Morinay

551   et al., 2019). Behavioural response to human presence has been used to measure boldness, for

552   instance through return latency or flight distance, in different species (e.g. Evans et al., 2010,

553   Barnett et al., 2012; Carrillo et al., 2013; Traisnel & Pichegru, 2018), including another

554   population of collared flycatchers (Garamszegi et al., 2015). Yet, individuals have been found

555   to adopt different context-dependent responses depending on the nature of predation risk, i.e.

556   the type of predators (e.g. different responses to ground and aerial predators in relation to nest

557   height: Kleindorfer et al., 2005). The risk associated with humans and nest predators such as

558   those used here is likely to strongly differ for both adults and broods in our study species, as

559   supported by partially different alarm calls in response to these two predator types (T. Tamin

560   and B. Doligez, pers. obs.). In addition, we cannot exclude that individual response was

561   altered here by habituation to human presence due to the frequent visits in the study patches to

562   collect breeding data on this population and on tit populations breeding in nearby nestboxes.

563   Using a boldness score measured in a natural nest predation context, we expect the boldness-

564   aggressiveness syndrome described here to better reflect the result of selective pressures in

565   this population. Boldness measures in response to human perturbations could however be

566   more relevant in an urban ecology context with different sources of risk and associated

567   selective pressures.

568   Conversely, boldness score was not correlated with neophobia score here. Among

569   personality traits, neophobia is frequently considered as part of the exploration axis (Réale et

570   al., 2007, 2010). Exploration behaviour is usually measured by how an individual interacts

571 with known features when placed in a novel (unknown) environment (Yoshida et al., 2005;

572 Brown et al., 2007; Cote et al., 2010a). In exploration situations in nature, individuals may

573 however be expected to both interact with unknown features and face increased known risks.

574 This may lead to the previously reported correlations between exploration behaviour or

575 neophobia and boldness (Appendix, Table A1). Our result however contrasts with these

576 previous observations and this could suggest that the relation between behavioural responses

577 in the context of unknown (exploration behaviour / neophobia) *vs.* known (boldness) risk may

578 be context-dependent. Our neophobia test here may have involved different direct costs for

579 adults in terms of energy or missed foraging opportunities compared to when neophobia is

580 measured using new objects placed near food resources or new food resources. Responses to

581 different behavioural tests under known or unknown risk could rely on different mechanisms

582 linked to metabolic rate and energy mobilisation, possibly regulating the general proactive-

583 reactive continuum. This could explain the absence of a general behavioural syndrome

584 involving neophobia in our case, while boldness and aggressiveness are linked, but this

585 remains to be explored.

586

587 *Fitness consequences of the boldness-aggressiveness syndrome*

588 The correlation between boldness and aggressiveness is among the most widely

589 studied behavioural correlations in the wild (see review in Sih & Bell, 2008). Although very

590 few studies directly investigated whether this phenotypic correlation resulted from among-

591 individual correlation, it may reflect a widespread behavioural syndrome (see Brommer &

592 Class, 2017). This suggests that certain combinations of boldness and aggressiveness levels

593 allow individuals to achieve higher reproductive success and/or survival compared to when

594 displaying a given level of each trait separately. Such combinations would thus be favoured

595 by natural selection, leading to a functional integration between both traits (Duckworth et al.,

24

596 2009; Dingemanse & Réale, 2005; Wolf & Weissing, 2012). Both boldness and

597 aggressiveness have independently been shown to affect fitness (for boldness, see Table S1;

598 for aggressiveness: see e.g. Ariyomo & Watt, 2012; Betini & Norris, 2012) but the links

599 between a boldness-aggressiveness syndrome and fitness components, in particular

600 reproductive success, remained unexplored thus far. Bold individuals were previously found

601 to achieve higher reproductive success compared to shy individuals (Appendix Table A1;

602 Smith & Blumstein, 2008) and this was suggested to result from higher foraging success

603 (Short & Petren, 2008; but see Barnett et al., 2012). If high aggressiveness requires more

604 energy to face agonistic confrontations with competitors, high boldness may allow individuals

605 to sustain this increased demand, and thereby secure a better access to higher quality

606 resources, including breeding territory / site, at the end of competitive processes. In turn,

607 access to high quality resources through increased aggressiveness may facilitate the

608 exploitation of these resources by bold individuals, in a positive feedback loop. Such

609 mechanisms may explain how an aggressiveness-boldness syndrome could provide fitness

610 benefits beyond the mere effects of the two traits separately.

611   The boldness-aggressiveness syndrome found here was potentially under selection

612 since our combined measure of both traits (the first principal component of the PCA with the

613 three behavioural traits under study, as used by previous studies: Cote et al., 2010a; Budaev,

614 2010; McEvoy et al., 2015) was linked with short-term reproductive success (i.e. at fledging).

615 Interestingly, this link was observed here in the quasi-absence of nest predation in this

616 population (Doligez & Clobert, 2003), showing that it was not directly due to lower nest

617 predation rate via increased nest defence, but should indeed result from other potential

618 benefits of the two behavioural traits combined. Yet, when the syndrome was measured using

619 the direct interaction between the two traits, no such link was found anymore. The origin of

620 this difference between these two measures of our syndrome is unclear at this stage, but it

621   calls for caution when predicting the selection consequences of the link with this fitness

622   component. While the first principal component leaves much among-individual behavioural

623   variation unexplained, modelling the syndrome with a simple interaction between both traits

624   may not capture the complex synergetic effects of the traits. Furthermore, the structuration of

625   the syndrome was straightforward here (two main traits involved) but with more than two

626   traits involved, interpreting both principal component axes and high-level interactions may be

627   difficult. Building standard operational scores to quantitatively estimate behavioural

628   syndromes allowing us to investigate their fitness consequences remains a challenge for future

629   studies. Furthermore, possible links between our aggressiveness-boldness syndrome and

630   reproductive success could also be indirect, via the simultaneous effect of a third variable on

631   both the expression of the syndrome and reproductive success, such as individual motivation

632   or condition. Future work is thus needed to unravel the exact causal mechanisms leading to

633   possible fitness benefits and thus underlying potential selection for the aggressiveness-

634   boldness syndrome in this and other populations, even though this syndrome should not

635   respond to selection here because the traits involved are not heritable.

636   Importantly, the sample on which boldness and thus the behavioural syndrome was

637   measured was biased towards successful pairs, i.e. pairs that reached the late (13 days old)

638   nestling stage, because of the practical implementation (timing) of behavioural tests in the

639   field. This may reduce the variation observed in the syndrome level in relation with

640   reproductive success, and thereby reduce our ability to detect such a link with success (for

641   personality-based sampling bias, see Biro & Dingemanse, 2009, Garamszegi et al., 2009).

642   Whether selection on the observed syndrome may translate into longer term evolution should

643   depend on (i) the extent to which the traits concerned are (both genetically and non-

644   genetically) transmitted to offspring but also (ii) the link with other fitness components, in

645   particular survival, including offspring survival until recruitment. Here, we found no link

646   between the boldness-aggressiveness syndrome and local recruitment probability, thus we

647   cannot exclude compensation of lower fledgling success for less aggressive and shyer parents

648   via higher juvenile survival after fledging, leading to no overall link between syndrome and

649   long-term reproductive success. Yet, even under such compensations, differential effects on

650   different fitness components may still have evolutionary consequences. Boldness and

651   aggressiveness may be linked to fitness through different ways: aggressiveness could favour

652   individual settlement and mating through competition for high quality nest sites (flycatchers

653   do usually not defend an all-purpose territory but only the immediate surroundings of a

654   breeding site; Cramp & Perrins, 1993), while boldness may be more generally associated to

655   foraging ability (e.g. Short & Petren, 2008) as well as defense under predator threats

656   (Kleindorfer et al., 2005), and thus survival. Assessing the synergetic impact of boldness and

657   aggressiveness for behavioural syndrome evolution will thus require a thorough investigation

658   of different fitness components and ultimately lifetime reproductive success. Importantly,

659   selection may operate on the ability to jointly adjust the behavioural traits displayed in a

660   syndrome to maximise fitness given individual and environmental conditions, i.e. on joint

661   phenotypic plasticity for boldness and aggressiveness here, rather than on the syndrome itself.

662   Even though each trait was not heritable separately in our case, which prevents the syndrome

663   to directly respond to selection, whether the joint plasticity in the expression of the traits is

664   heritable is currently unknown (see Henriksen et al., 2020). More work will be needed to fully

665   apprehend the long-term fitness consequences of the boldness-aggressiveness syndrome

666   described here and its plasticity, and thereby understand the mechanisms underlying its

667   evolutionary consequences in natural populations.

668

669

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Conflict of interest

The authors declare no competing interests.

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Table 1. Sources of variation in boldness score, measured in the context of nest defence against a nest predator

| | Within-year | | | | Between-year | | | |
| | With fixed effects | | Without fixed effects | | With fixed effects | | Without fixed effects | |
	PM	95% CI	PM	95% CI	PM	95% CI	PM	95% CI
Intercept	-2.71	[-9.85; 4.09]	2.09	[1.79; 2.38]	-0.63	[-7.05; 5.59]	2.28	[2.16; 2.38]
Fixed effects								
Sex (male)	**0.28**	**[0.15; 0.41]**			**0.28**	**[0.15; 0.40]**		
Age (yearling)	-0.03	[-0.16; 0.10]			-0.04	[-0.18; 0.09]		
Test order	**0.17**	**[0.07; 0.27]**						
Test date	0.09	[-0.19; 0.27]			0.07	[-0.09; 0.24]		
Test date²	-0.00	[-0.00; 0.00]			-0.00	[-0.00; 0.00]		
Presence of the partner (present)	**0.93**	**[0.68; 1.18]**						
Random effects								
$V_{individual}$	0.73	[0.61; 0.87]	0.79	[0.66; 0.93]	0.57	[0.39; 0.77]	0.60	[0.41; 0.80]
$V_{observer}$	0.30	[0.15; 0.49]	0.29	[0.14; 0.47]				
$V_{year-patch}$	0.05	[0.01; 0.11]	0.06	[0.01; 0.12]	0.13	[0.06; 0.21]	0.14	[0.07; 0.22]
V_{dummy}	0.13	[0.02; 0.32]	0.13	[0.02; 0.30]	[			
V_{ε}	0.68	[0.59; 0.77]	0.70	[0.61; 0.80]	0.59	[0.42; 0.77]	0.59	[0.43; 0.76]
Number of observations	2101		2101		1384		1384	
Effective sample size	>3440		>2248		>2800		>2700	

1033   Estimates for random effects are shown with and without fixed effects, and for the within- and between-year (i.e. all test values vs. one average

1034   value per individual per year) models. Posterior modes (PM) and 95% credible intervals (CI) are given. For categorical fixed effects, estimates

1035   refer to the category indicated within parentheses. $V_{individual}$ ($N = 1228$ with and without fixed effects) $V_{observer}$ ($N = 27$), $V_{year-patch}$ ($N = 75$), V_{dummy}

1036   ($N = 10$) and V_{ε} for within-year models indicate the variance associated to the individual identity, observer, the combination of year and patch,

1037 dummy and the residual variance, respectively, with $V_{individual}$ ($N = 1204$ with and without fixed effects), $V_{year-patch}$ ($N = 75$) and V_ε for between-

1038 year models the variance associated to individual identity, the combination of year and patch and the residual variance respectively. Estimates

1039 whose 95% CI do not encompass zero are shown in bold; fixed and random effects not estimable in between-year models are left empty.

1040   **Table 2.** Variance explained by the two principal components in the PCA of the three

1041   behavioural traits

	Principal components	
Behavioural traits	PC1	PC2
Aggressiveness	**0.75**	-0.29
Neophobia	-0.01	**0.95**
Boldness	**0.80**	0.23
Proportion of variance explained	0.40	0.35

1042

1043   Variance explained and component loadings ($N = 688$) for the three behavioural traits under

1044   study. Loadings above the threshold of 0.32 are shown in bold.

1045 **Table 3.** Phenotypic correlation between boldness, aggressiveness and neophobia scores and

1046 its components, i.e. among- and within-individual and environmental correlations

Traits considered	N	Phenotypic correlation	Among-individual correlation	Common-environ correlation
Boldness / Aggressiveness	979	**0.16 [0.08; 0.22]**	**0.42 [0.02; 0.86]**	0.12 [-0.32;
Boldness / Neophobia	694	-0.00 [-0.11; 0.08]	-0.00 [-0.67; 0.53]	-0.00 [-0.52;

1047

1048 Number of observations (N), posterior modes and 95% credible intervals (CI) are given.

1049 Estimates whose 95% CI do not encompass zero are shown in bold.

46

Figures

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1053 **Figure 1.** Graphical representation summarising the timing along the breeding season and

1054 main features of the three experimental tests: context, trait measured, stimulus used (with

1055 numbers of sets used to avoid pseudoreplication), timing of the test (breeding phase and time

1056 of the day), test duration, mode of recording and score computed. The red arrows indicate

1057 how many tests could be performed in each case (up to 4 for the aggressiveness test, 1 for the

1058 neophobia test and up to 2 for the boldness test) and their timing (maximum one test per day

1059 in the sequence). The red circles show an illustration of the stimulus used in each case (here, a

1060 pair of dummy flycatchers for the aggressiveness test, one at the nest entrance and one on the

1061 roof (for interspecific competition, only one great tit dummy was used, placed at the nestbox

1062 entrance), accompanied by the broadcast of the song of the species concerned; a blue and red

1063 7-cm high plastic figurine for the neophobia test; and a red squirrel for the boldness test). The

1064 timing of breeding phases is illustrated for an average year here but could vary depending on
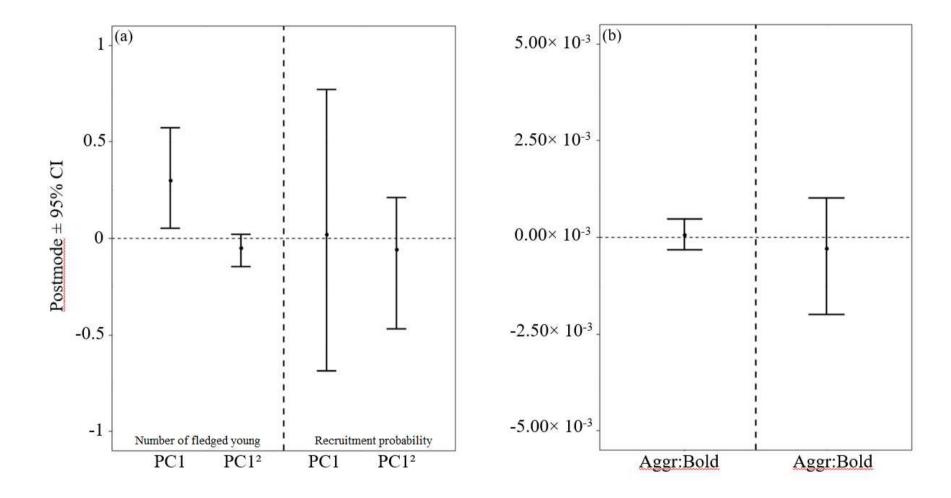
1065 years.

1066

1067 **Figure 2.** Posterior mode and 95% CI of the effect of the boldness-aggressiveness syndrome

1068 measured by (a) the first principal component of the PCA between the three behavioural

1069 scores considered here, boldness, aggressiveness and neophobia (PC1) and its square value

1070 (PC1²) or (b) the interaction between the aggressiveness and boldness scores (denoted

1071 aggr:bold) on the number of fledged young and their recruitment probability. Estimates were

1072 obtained over the 100 randomisations used to select one parent randomly when both were

1073 scored (see text).

1074

1075 **Figure 3.** Number of fledged young depending on the first principal component of a PCA

1076 between the three behavioural scores considered here (boldness, aggressiveness, neophobia)

1077 as a measure of the boldness-aggressiveness syndrome. We present for illustration here one of

1078 the 100 randomisations used to select one parent when both were scored (see text). Data

1079 points as well as posterior mode (line) ± 95% credible interval (grey area) of the estimate

1080 coefficient are shown; estimates were obtained from the model including the first principal

1081 component, its squared value, sex, age, laying date and laying date^2 as fixed effects, and

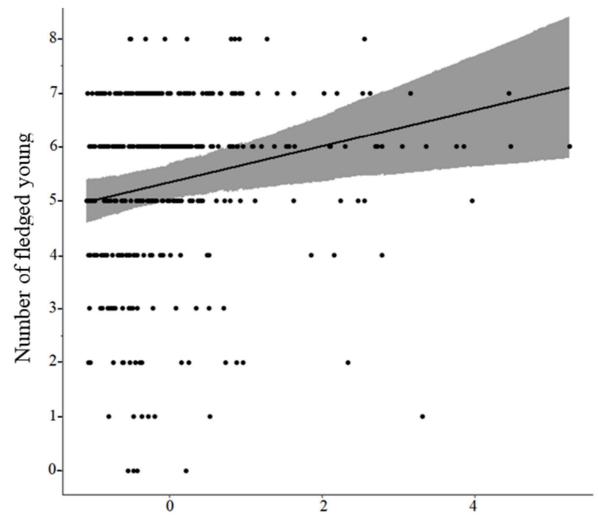1082 individual identity and the combination between patch and year as random factors.

1083 Figure 1

1084

Test	1 - AGGRESSIVENESS	2 - NEOPHOBIA	3 - BOLDNESS
Context	Behaviour towards competitors (social situation) involving no deadly risk	Behaviour towards a new (nonsocial) situation involving unknown risk	Behaviour towards a dangerous (nonsocial) situation involving known deadly risk
Trait measured	Agonistic response to a simulated competitor intrusion	Response to the presence of a novel object in a known environment	Risk-taking response to a simulated nest predator attack
Stimulus	Dummy intra- (flycatcher pair) or inter- (great tit) specific competitor at the nestbox entrance (and roof) + song broadcast – 8 different decoy sets / 5 different song broadcast tracks	Coloured plastic figurine beside the nestbox entrance	Dummy of a nest predator (squirrel for all years or woodpecker only in 2011) at the nestbox entrance – 8 different squirrel dummies / 4 different woodpecker dummies
Timing	Second half of the nest building up to early laying (for late nests) - from 0600 to 1300	Early nestling stage (day 5-6 posthatching) - from 0600 to 1400	Late nestling stage (day 13-14 posthatching) - from 0600 to 1300
Total test duration	15 min (+5 min if a (or both) parent(s) arrived after 10 min to record each during > 5 min)	2 consecutive 1-hour periods: (1) without novel object, (2) with novel object	Up to 15 min (adjusted to the time of arrival of both parents to record each during 5 min)
Recording	Observer (camouflaged 8-10 m from the nestbox)	Video recorder (camouflaged 6-8 m from the nestbox)	Observer (camouflaged 8-10 m from the nest box)
Score	Number of movements within 2 m from the nest box and agonistic behaviours recorded during > 5 min	Latency to resume feeding after human disturbance in presence of a novel object / latency in absence of the novel object	Number of movements and attack behaviours within 2 m from the nest box recorded during 5 min

<u>Figure 3</u>