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

3

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22 **Key-words:** Among- and within-individual correlations – behavioural tests – collared
23 flycatcher – *Ficedula albicollis* – fledging success – heritability – neophobia – personality
24 traits – recruitment – repeatability

25 **Running title:** Behavioural syndrome and reproductive success

26

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.

50 **Introduction**

51

52 Predation has long been recognized as a major evolutionary pressure shaping life-
53 history strategies in the wild (e.g. in birds: Ricklefs, 1970; Oro et al., 1999; Martin & Briskie,
54 2009; in fish: Strauss, 1990; in arthropods: Caramujo et al., 1997). The behavioural response
55 of individuals to predation threats has therefore received much attention. The propensity to
56 take risks in a well-identified dangerous situation such as a predator attack defines boldness
57 (Kleindorfer et al., 2005; Réale et al., 2007; Barnett et al., 2012). Due to the potential
58 consequences of taking risks when defending oneself or one's young, boldness level can be
59 expected to be under strong selective pressures (Traisnel & Pichegru, 2018; see also
60 Dingemanse & Réale, 2005). Boldness has been found to positively associate with individual
61 fitness components, such as survival (e.g. Richardson et al., 2019) and reproductive success,
62 including mating success (e.g. Reaney & Backwell, 2007; Ward-Fear et al., 2018) and
63 offspring number and/or condition (e.g. Bubac et al., 2018; Hollander, Van Overveld, Tokka,
64 & Matthysen, 2008). Yet boldness also incurs costs, such as increased injury risk and
65 individual mortality (Claireaux et al., 2018; Ward-Fear et al., 2018), and/or increased
66 metabolic rate (Mathot, Dingemanse & Nakagawa, 2019) and daily energy expenditure
67 (Careau, Thomas, Humphries & Réale, 2008). Thus selection should favour the adjustment of
68 boldness level depending on its costs and benefits balance as a function of other phenotypic
69 traits in given environmental conditions (Richardson et al., 2019). Understanding the
70 consequences of the interplay between boldness and other phenotypic traits on fitness in the
71 wild therefore represents a major research theme in behavioural ecology.

72 The interdependence of suites of phenotypic traits has been under recent focus in
73 natural populations, in particular as a mechanism underlying the maintenance of among-
74 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.

137

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

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

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

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

249 *Ethical Note*

250 Permission for catching and ringing adults and nestlings (approximately 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

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

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 date² 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

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):

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

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

354 where $Cov_{indA,indB}$, $Cov_{envA,envB}$ and $Cov_{\epsilon A,\epsilon B}$ 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 Link between syndrome and reproductive success: univariate GLMMs

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 Bayesian procedures

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: $V = 1$, $v = 1$, $\alpha\mu = 0$, $\alpha V =$
419 1000 ; bivariate models: $V = \text{diag}(2)$, $v = 2$, $\alpha\mu = c(0,0)$, $\alpha V = \text{diag}(2)$). 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

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

472 of fledged young (posterior mode [95% CI]: -0.05 [-0.15; 0.02]; Fig. 2a). When directly
473 modelling the syndrome with the interaction between aggressiveness and boldness, the
474 number of fledged young was not related to the interaction (posterior mode [95% CI]:
475 6.33×10^{-5} [-3.28×10^{-4} ; 4.58×10^{-4}]; Fig. 2b). In addition, the number of fledged young was
476 linked to neither aggressiveness nor boldness when included separately as fixed effects
477 (posterior mode [95% CI] for aggressiveness: 0.007 [-0.002; 0.015], for boldness: 0.007 [-
478 0.001; 0.015]). None of the other fixed effects were related to the number of fledged young
479 (Appendix Table A7).

480 The probability of recruitment was related to neither the first principal component
481 (posterior mode [95% CI]: 0.02 [-0.69; 0.77]) nor its squared value (posterior mode [95% CI]:
482 -0.06 [-0.47; 0.21]) over randomisations (Fig. 2a). When directly modelling the syndrome
483 with the interaction between aggressiveness and boldness, the probability of recruitment was
484 not related to the interaction (posterior mode [95% CI]: -0.0003 [-0.002; 0.001]; Fig. 2b); it
485 was not related to aggressiveness or boldness when included separately either (posterior mode
486 [95% CI]: for aggressiveness: -0.003 [-0.03; 0.02], for boldness: -0.003 [-0.03; 0.02]). Again,
487 none of the other fixed effects were related to the probability of recruitment (Appendix Table
488 A7).

489

490

491 **Discussion**

492

493 Boldness is a crucial trait shaping responses to risky situations. Yet, the fitness
494 consequences of the frequently observed relations between boldness and other traits remain
495 poorly explored in empirical studies. In a natural population of collared flycatchers, we
496 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.,

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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682

683 **Conflict of interest**

684 The authors declare no competing interests.

685

686

687 **References**

688

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1031 **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 date ²	-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								
$V_{\text{individual}}$	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]				
$V_{\text{year-patch}}$	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	

1032

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. $V_{\text{individual}}$ ($N = 1228$ with and without fixed effects) V_{observer} ($N = 27$), $V_{\text{year-patch}}$ ($N = 75$), 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 $V_{\text{individual}}$ ($N = 1204$ with and without fixed effects), $V_{\text{year-patch}}$ ($N = 75$) 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

Behavioural traits	Principal components	
	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	<i>N</i>	Phenotypic correlation	Among-individual correlation	Common-environmental correlation
Boldness / Aggressiveness	979	0.16 [0.08; 0.22]	0.42 [0.02; 0.86]	0.12 [-0.32; 0.56]
Boldness / Neophobia	694	-0.00 [-0.11; 0.08]	-0.00 [-0.67; 0.53]	-0.00 [-0.52; 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.

1050 **Figures**

1051

1052

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) \pm 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 date² 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

1085 Figure 2

1086



