



HAL
open science

No evidence for behavioural syndrome and genetic basis for three personality traits in a wild bird population

Jennifer Morinay, Grégory Daniel, Lars Gustafsson, Blandine Doligez

► To cite this version:

Jennifer Morinay, Grégory Daniel, Lars Gustafsson, Blandine Doligez. No evidence for behavioural syndrome and genetic basis for three personality traits in a wild bird population. *Animal Behaviour*, 2019, 153, pp.69-82. 10.1016/j.anbehav.2019.05.001 . hal-02413241

HAL Id: hal-02413241

<https://hal.science/hal-02413241v1>

Submitted on 24 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **No evidence for behavioural syndrome and genetic basis for three**
2 **personality traits in a wild bird population**

3

4

5 **Jennifer Morinay^{1,2,*}, Gregory Daniel¹, Lars Gustafsson², Blandine Doligez¹**

6

7 ¹ Université de Lyon, Université Lyon 1, CNRS, Laboratoire de Biométrie et Biologie
8 Evolutive UMR 5558, Villeurbanne, France

9 ² Department of Ecology and Evolution/Animal Ecology, Evolutionary Biology Centre,
10 Uppsala University, Uppsala, Sweden

11

12 Received 3 September 2018

13 Initial acceptance 31 October 2018

14 Final acceptance 25 March 2019

15 MS number 18-00633R

16

17 * *Correspondence:* J. Morinay, LBBE, CNRS UMR 5558, Univ Lyon–Université Claude
18 Bernard Lyon 1, Bâtiment Gregor Mendel, 43 boulevard du 11 novembre 1918, 69622
19 Villeurbanne Cedex, France.

20 E-mail address: jennifer.morinay@gmail.com

21

22

23 **Keywords:** aggressiveness, between- and within-individual correlations, boldness, collared
24 flycatcher, *Ficedula albicollis*, heritability, neophobia, parental effects, pedigree, quantitative
25 genetics, repeatability

26 **ABSTRACT**

27

28 Personality traits and their correlations have been shown to be linked with life history
29 strategies and fitness in various species. Between-individual correlations (i.e. behavioural
30 syndromes) between personality traits can affect the evolutionary responses of these traits to
31 environmental variation. Understanding the genetic and ecological determinants of
32 personality traits and their interactions as behavioural syndromes in the wild is thus needed to
33 shed light on the mechanisms shaping their evolution. Partitioning the observed (co)variance
34 in these traits, however, requires large numbers of repeated behavioural measures on many
35 individuals of known relatedness level. In the absence of such data, it is thus often assumed
36 that phenotypic (co)variances inform about (1) underlying between-individual (co)variances
37 (i.e. ignoring within-individual (co)variances) and (2) underlying genetic (co)variances. We
38 tested these assumptions using three personality traits collected during 3 years on a long-term
39 monitored breeding population of collared flycatchers, *Ficedula albicollis*. We partitioned the
40 observed phenotypic (co)variance of aggressiveness, boldness and neophobia into genetic,
41 permanent environment and parental components, and we estimated the repeatability and
42 heritability of these traits and their between-individual correlations. All three traits were
43 repeatable between years (at least on the latent scale) but none were heritable. Permanent
44 environment effects explained 15% of the phenotypic variance in aggressiveness, and parental
45 effects explained 25% of the phenotypic variance in neophobia, in line with previous studies
46 in wild populations. The three traits showed phenotypic correlations but no between-
47 individual correlations and no additive genetic covariance. Thus, our results did not support
48 the assumptions that phenotypic covariance reflects behavioural syndromes and genetic
49 covariance. We discuss the reasons for the absence of heritability and between-individual and

50 genetic covariance between these three personality traits in light of the possible selective
51 pressures acting on this population.

52

53

54 **INTRODUCTION**

55

56 Over the past two decades, personality traits, that is, repeatable between-individual
57 behavioural differences across time and contexts (Réale, Reader, Sol, McDougall, &
58 Dingemanse, 2007), have received increasing attention in animal behavioural and
59 evolutionary ecology studies (Bell, 2007; Bell, Hankison, & Laskowski, 2009; Carere &
60 Maestriperi, 2013; Dingemanse & Réale, 2005; Réale et al., 2007; Sih, Bell, & Johnson,
61 2004; Sih, Bell, Johnson, & Ziemba, 2004). Five ecologically important personality axes have
62 been identified to characterize the behavioural responses of individuals when interacting with
63 their environment (activity, exploration, boldness) and with others (aggressiveness,
64 sociability; Réale et al., 2007). Personality traits have been shown to depend on ecological
65 parameters (e.g. Réale et al., 2007; Sih, Cote, Evans, Fogarty, & Pruitt, 2012), to be heritable
66 (e.g. van Oers, de Jong, van Noordwijk, & Drent, 2005; van Oers & Sinn, 2013), to be linked
67 to life history traits or fitness (Dingemanse, Both, Drent, & Tinbergen, 2004; Dingemanse &
68 Réale, 2013; Duckworth & Kruuk, 2009; Reale et al., 2010; Schuett, Tregenza, & Dall, 2010;
69 Smith & Blumstein, 2008) and often to correlate with each other at the individual level,
70 forming so-called behavioural syndromes (Garamszegi, Markó, & Herczeg, 2012; Andrew
71 Sih, Bell, & Johnson, 2004; van Oers & Sinn, 2013). Such correlations may result from a
72 functional integration of personality traits favoured by selection when interactions between
73 these traits increase individuals' fitness in given environmental conditions (e.g. Dingemanse
74 et al., 2007). Altogether, these various results reveal the crucial role that personality traits may

75 play in shaping evolutionary processes in wild populations (Dingemanse et al., 2004;
76 Duckworth & Badyaev, 2007; Karlsson Green, Eroukhmanoff, Harris, Pettersson, &
77 Svensson, 2016; Niemelä, Lattenkamp, & Dingemanse, 2015).

78 Understanding the evolution of personality traits and their associations in behavioural
79 syndromes requires understanding the mechanisms underlying these between-individual
80 differences in behaviour and their interactions, including their genetic basis. Phenotypic
81 correlations between personality traits result from the addition of between-individual
82 correlations (defining behavioural syndromes per se, whether genetic or nongenetic) and
83 within-individual (or residual) correlations (Brommer, 2013; Dingemanse & Réale, 2013;
84 Dingemanse, Kazem, Réale, & Wright, 2010). Assessing the relative contribution of between-
85 and within-individual correlation components in observed phenotypic correlations can be
86 crucial because between-individual correlations may constrain the independent evolution of
87 the traits involved and thus may have major evolutionary consequences in the wild (Sih, Bell,
88 & Johnson, 2004).

89 To reliably quantify this relative contribution of between- and within-individual
90 correlations, multiple measurements of the personality traits considered must be collected on a
91 large number of individuals. When only single measurements are available, it is often
92 assumed that a phenotypic correlation observed between personality traits reflects an
93 underlying between-individual correlation, i.e. the within-individual correlation is negligible
94 (the so-called ‘individual gambit’, Brommer, 2013). Furthermore, to quantify genetic variance
95 in personality traits and genetic covariance between them, the level of genetic relatedness
96 between individuals measured has to be incorporated (e.g. via pedigree information) in the
97 models. When relatedness information is unavailable, it is often assumed that the observed
98 phenotypic (co)variance reflects the underlying genetic (co)variance (the so-called

99 'phenotypic gambit'; Grafen, 1984; Hadfield, Nutall, Osorio, & Owens, 2007; van Oers &
100 Sinn, 2011).

101 These two crucial assumptions have been tested empirically in various species, and
102 recent meta-analyses including over 30 studies, among which 25 are from wild populations,
103 have confirmed their overall validity (Brommer & Class, 2017; Dochtermann, 2011;
104 Dochtermann, Schwab, & Sih, 2015). Across these studies, the sign (and to a certain extent
105 the magnitude) of the phenotypic correlations between personality traits reliably informed on
106 the sign (and the magnitude) of the between-individual correlations (Brommer & Class, 2017)
107 and of the genetic correlations (Dochtermann, 2011). Furthermore, 52% of the between-
108 individual variation in personality traits taken separately was explained by additive genetic
109 variance (Dochtermann et al., 2015). A recent empirical study on a wild population of yellow-
110 bellied marmots, *Marmota flaviventris*, estimated the proportion of phenotypic (co)variance
111 explained by genetic, permanent environment and maternal (co)variances between four
112 different personality traits: docility, exploration, activity and sociability (Petelle, Martin, &
113 Blumstein, 2015). Results showed additive genetic variations, as well as maternal and
114 permanent environment variations, in all four traits and a positive genetic correlation between
115 activity and sociability (Petelle et al., 2015). More of such integrative studies partitioning the
116 observed phenotypic (co)variance in multiple personality traits simultaneously are needed in
117 different biological models with contrasting life histories to better understand the mechanisms
118 underlying and possibly constraining the evolution of correlated personality traits.

119 In this study, we assessed the genetic basis of three personality traits, together with the
120 relative contribution of between- and within-individual variations in, and correlations
121 between, these traits, chosen for their potentially important effects on crucial ecological
122 processes (here, nest site acquisition and defence against competitors and predators) in a
123 natural population of a small territorial, short-lived, migrant passerine bird, the collared

124 flycatcher, *Ficedula albicollis*. During 3 consecutive years, we measured for several hundreds
125 of breeding pairs in the field (1) aggressiveness towards competitors (as the agonistic reaction
126 to simulated territorial intrusions by intra- and interspecific competitors), (2) boldness
127 towards predators (as the latency to resume nestling feeding after human disturbance) and (3)
128 neophobia, possibly reflecting exploration (as the latency to resume nestling feeding in the
129 presence of a novel object on the nest site; following Réale et al.'s 2007 definitions). To
130 identify the mechanisms underlying the phenotypic (co)variation in these behavioural traits,
131 we assessed to what extent (1) additive genetic, parental or permanent environment effects
132 contributed to the observed phenotypic (co)variance, while accounting for fixed individual
133 (sex, age) covariates, and (2) between-individual correlations explained phenotypic
134 correlations between these three traits. Based on many previous studies on personality traits in
135 populations of passerines of similar ecology (e.g. Dingemanse, Both, Drent, van Oers, & van
136 Noordwijk, 2002; Drent, Oers, & Noordwijk, 2003; Duckworth & Badyaev, 2007;
137 Garamszegi et al., 2015; Garamszegi, Rosivall, et al., 2012; van Oers, Drent, de Goede, & van
138 Noordwijk, 2004), we expected heritable differences to partly explain variation in
139 aggressiveness, boldness and neophobia in our study population. Furthermore, high
140 aggressiveness, high boldness and low neophobia may allow individuals to efficiently secure
141 and defend a breeding site when they are unfamiliar with the environment (e.g. for dispersers:
142 Cote, Clobert, Brodin, Fogarty, & Sih, 2010; Duckworth & Kruuk, 2009; Korsten, van
143 Overveld, Adriaensen, & Matthysen, 2013). Thus we predicted a functional integration and
144 (possibly genetically based) between-individual correlations between these traits. In another
145 population of collared flycatchers, male aggressiveness and boldness, but not neophobia, were
146 found to be phenotypically correlated in some years (Garamszegi et al., 2015; Garamszegi,
147 Eens, & Török, 2009). This population and ours, however, differ greatly in both demographic
148 functioning (e.g. male age structure: Hegyi, Rosivall, & Török, 2006) and selective pressures

149 (e.g. nest predation: Doligez & Clobert, 2003; sexual selection: Qvarnström, 1997; see also
150 Rosivall, Török, Hasselquist, & Bensch, 2004), which may affect the fitness consequences of
151 interactions between personality traits, and thus their potential functional integration.

152

153

154 **METHODS**

155

156 *Study species and population monitoring*

157 Collared flycatchers are migratory cavity nesters and readily breed in artificial nestboxes,
158 providing easy access to parents' identity and breeding data. Between 2011 and 2013, we
159 conducted the behavioural tests (see below) on 1131 pairs breeding in nestboxes spread over
160 14 to 22 forest patches in our study population located on the island of Gotland (Sweden,
161 Baltic Sea). Each year since 1980, nests in boxes have been monitored at least weekly from
162 late April until early July, allowing us to record major breeding variables (laying and hatching
163 dates; clutch size; nestling number, condition and fledging success). Breeding pairs were
164 captured, identified and ringed if previously unringed; females were caught during incubation
165 and males while feeding nestlings. Nestlings were ringed between day 8 and day 13 after
166 hatching; fledging typically occurs 16 days after hatching. Adult and nestling identification
167 every year combined with a high return rate of both adults (approximately 40%) and juveniles
168 (approximately 10%) for such a short-lived passerine bird (Gustafsson, 1989) allowed us to
169 establish a high-quality social pedigree of the population which has previously been used in
170 several quantitative genetic studies (e.g. Evans & Gustafsson, 2017; Merilä & Sheldon, 2000;
171 Sheldon, Kruuk, & Merilä, 2003; Appendix Table A1). In this population, approximately 15%
172 of all nestlings are extrapair (Sheldon & Ellegren, 1999), a percentage considered low enough
173 for quantitative genetic models to provide valid (i.e. only slightly underestimated) heritability

174 estimates from the social pedigree (Charmantier & Réale, 2005; Firth, Hadfield, Santure,
175 Slate, & Sheldon, 2015), even though no information is available yet on how extrapair
176 paternity may affect genetic covariances. The clear sexual dimorphism in plumage coloration
177 in this species allowed an easy discrimination of adult males (black and white plumage with a
178 white forehead patch) from females (brown plumage; Svensson, 1992), even from several
179 metres away during behavioural tests. Adults could also be aged by plumage criteria
180 (yearlings versus older adults; Svensson, 1992).

181

182 *Aggressiveness score*

183 We measured the level of aggressiveness of breeding flycatchers soon after settlement, during
184 nest building or early laying, that is, when the risk of losing a nestbox to a competitor is
185 highest in this single-clutch species. During the breeding season, collared flycatchers compete
186 for nest sites with conspecifics but also with great tits, *Parus major*, the second most abundant
187 species breeding in nestboxes in the study area (Gustafsson, 1987). Aggressiveness towards
188 conspecific intruders was shown to decrease after the start of incubation (Král & Bícík, 1989)
189 even though aggressiveness towards great tit intruders remained high throughout the breeding
190 cycle (Král & Bícík, 1992). To elicit an aggressive response from a focal flycatcher pair, we
191 simulated the intrusion of competitors at the nest of the pair by attaching to its nestbox clay
192 decoys mimicking either a flycatcher pair or a single (male) great tit. We used a pair (one
193 male and one female) for flycatcher decoys to elicit and measure an aggressive response by
194 both pair members, that is, to avoid a sex-specific response towards this intraspecific
195 stimulus, while the response to the interspecific stimulus (great tit decoy) was not expected to
196 differ depending on the sex of the decoy. In addition, we simultaneously broadcast male songs
197 corresponding to the decoy(s) species with a loudspeaker placed just under the nestbox. To
198 avoid pseudoreplication, we randomly used one of eight different sets of decoys and one of

199 five different song tracks per species for each test. After attaching the decoys to the nestbox
200 and the loudspeaker under the box, the observer sat under a camouflage net approximately 8–
201 10 m away from the nestbox and recorded the following behaviours for each pair member: (1)
202 movements between perches and perching position (within 2 m, between 2 and 5 m or
203 between 5 and 10 m away from the nestbox), (2) agonistic behaviours towards a decoy
204 (attacks and stationary flights in front of the decoy) and (3) chases towards living birds
205 attracted by the stimulus. A behavioural test started with an observation period of 15 min but
206 we lengthened the test by up to 5 min when an individual arrived between 10 and 15 min after
207 the start of the test, and up to 5 additional min if its partner arrived during this extra time, so
208 that we could observe the behavioural response of each pair member for at least 5 min. Each
209 test thus lasted between 15 and 25 min. If an individual was observed during less than 5 min
210 before the end of the test, it was discarded from the analyses and these observations were
211 therefore not used later on.

212 Aggressiveness level was measured as the sum of the number of movements within 2
213 m of the nestbox, attacks, stationary flights and chases. We included this latter behaviour
214 because chasing a live intruder may have prevented the focal flycatcher from interacting with
215 the decoy, while reflecting an aggressive territory defence response. The number of each type
216 of behavioural response (movements, agonistic behaviours and chases) was standardized by
217 the time interval between the first observation of the individual and the end of the test,
218 rescaled to 15 min. Using alternative scores did not qualitatively change the results (see
219 Appendix and Table A2). We conducted aggressiveness tests two to four times per focal pair
220 over a 5-day interval, with at most one test per day and tests on 2 days in a row. The stimulus
221 used (intra- / interspecific decoys) was alternated between tests after a random assignment for
222 the first test. An aggressiveness score was computed for each individual for each test. We
223 obtained aggressiveness responses (for more than 5 min at least once per year) for 1974

224 individuals (including unidentified ones; 961 females and 1014 males in 1046 nests). Among
225 those, 825 females and 667 males were later captured and identified, and thus used for
226 heritability estimation. In 601 breeding pairs both partners were identified and responded to
227 the tests and in 273 only one partner responded. We obtained repeated estimates for 502 and
228 445 identified females and males, respectively.

229

230 *Boldness and neophobia scores*

231 During nestling rearing, we estimated (1) boldness level by measuring the individual's
232 reaction towards the presence of a human observer near the nestbox and (2) neophobia level
233 by measuring the reaction towards the presence of a novel object on the nestbox (i.e. in a
234 familiar environment), following the definitions from Réale et al. (2007). As advised in
235 Greenberg and Mettke-Hofmann (2001), we measured our behavioural responses as the
236 latency to perform a highly motivating action (here, feeding their nestlings) after disturbance.
237 We conducted one combined boldness/neophobia test per breeding pair when the nestlings
238 were 5 days old, that is, at the beginning of the period of highest provisioning by parents (and
239 before we caught the parents to avoid any behavioural interference). A test consisted of two
240 consecutive periods of approximately 1 h each: the behaviour of the parents was recorded first
241 without any change in the surroundings of the nestbox, that is, without the novel object, and
242 second with a novel object (here a coloured figurine approximately 7 cm high) attached near
243 the entrance hole of the nestbox. Both periods were video-recorded from a distance (6–8 m).
244 At the beginning of each period, the observer checked the camouflaged video recorder,
245 walked to the nestbox, opened it to check nestling satiety, closed it, and then left the area. The
246 test was abandoned if the nestlings were very hungry to avoid them starving if the parents
247 were too disturbed by the test.

248 We estimated boldness score using the latency to enter the nestbox after the departure
249 of the observer in the first period (i.e. without the novel object). Reaction to disturbance by
250 humans has previously been used in boldness tests in this species (e.g. Garamszegi et al.,
251 2009). To ease interpretation (i.e. increasing values of boldness score corresponding to
252 increasing level of boldness), we transformed the latency to enter the nestbox such that the
253 boldness score of an individual was the maximum latency observed in the entire data set
254 minus the latency for this individual. We estimated neophobia score based on the latency to
255 enter the box after the departure of the observer in the second period (i.e. in the presence of
256 the novel object). For both boldness and neophobia scores, individuals that did not enter the
257 nestbox during the first period of the test were not used in the analysis (187 of 1251
258 observations, i.e. 15%). Individuals that entered the nestbox during the first but not the second
259 part of the test (411 of 1064 observations, i.e. 39%) were considered as the most neophobic
260 ones but could not be assigned a latency. To include them in the analyses, we discretized the
261 latency to enter the nestbox in the second period into four categories based on its quartiles,
262 assigning values from 1 to 4 for increasing latencies, and adding a fifth category including
263 individuals that did not enter in the second part of the test. Using alternative scores for
264 boldness and neophobia did not qualitatively change the results (see Appendix and Tables A2
265 and A3). We obtained boldness and neophobia estimates for 849 identified individuals (472
266 females and 378 males). Over the 3 years, we assessed 403 unique breeding pairs where both
267 identified partners responded to the tests and 185 pairs where only one partner responded. We
268 obtained repeated boldness and neophobia scores (i.e. several years in a row) for 66 females
269 and 65 males.

270

271 *Repeatability and heritability of aggressiveness, boldness and neophobia*

272 We estimated the repeatability of aggressiveness, boldness and neophobia scores as well as
273 their heritability by fitting three separate univariate animal models. The models included the
274 following random effects: additive genetic effect (associated with the pedigree), individual
275 identity for the repeated measures per individual (permanent environment effect), maternal
276 and paternal identities, forest patch, observer identity (the person observing and reporting the
277 behaviours onsite for the aggressiveness tests and the person extracting latencies from the
278 video recording for the boldness and neophobia tests). The models of the aggressiveness score
279 also included the broadcast song track and decoy set identifiers. In addition, the models
280 included the following fixed effects, to control for potential confounding factors: sex, age
281 (two levels: yearling versus older) and their interaction, as well as year (three levels: 2011,
282 2012, 2013). The aggressiveness model also included stimulus type (two levels: flycatcher
283 versus great tit decoys), the order of the test within a year (continuous variable: first to
284 fourth), the presence of the partner during the test (binary variable: yes/no) and the presence
285 of other live flycatchers or great tits (binary variable: yes/no). The boldness and neophobia
286 models included the number of ringed nestlings as a proxy of the motivation to enter the
287 nestbox to feed nestlings. The neophobia models included the boldness score to control for the
288 effect of the human disturbance at the beginning of the period with the novel object. All
289 continuous fixed terms were centred and standardized prior to analysis to allow comparisons
290 between effects.

291 Repeatabilities (R) were estimated as the ratio of the sum of the additive genetic (V_A),
292 permanent environment (V_{PE}), maternal and paternal identities variances (V_M and V_F ,
293 respectively) over the total phenotypic variance (V_P , sum of all variances; Falconer &
294 Mackay, 1996; with possibly an additional term accounting for the distribution variance,
295 Nakagawa & Schielzeth, 2010). Narrow-sense heritabilities (h^2) were estimated as the ratio of
296 the additive variance V_A over the phenotypic variance V_P . The presence of fixed effects in

297 models did not result in over- or underestimating repeatability and heritability estimates (as
 298 warned against in Nakagawa & Schielzeth, 2010), because estimates were similar when
 299 obtained from models with only the intercept (presented in the main text) and from models
 300 with the previously described fixed effects (see Appendix Tables A1, A2, A3; except for a
 301 slight overestimation of the boldness and neophobia repeatabilities on the latent scale). For
 302 aggressiveness, we also estimated within-year repeatability by replacing the additive genetic
 303 and permanent environment effects by a unique identifier per individual per breeding season.

304

305 *Correlations between aggressiveness, boldness and neophobia scores*

306 We estimated the between- and within-individual correlations between aggressiveness,
 307 boldness and neophobia scores by fitting a trivariate mixed-effects model (Dingemanse &
 308 Dochtermann, 2013). For this model, aggressiveness was averaged over all aggressiveness
 309 scores of an individual in a given year (i.e. over up to four estimates). We chose this
 310 averaging approach because aggressiveness score (1) differed depending on decoy species,
 311 chosen at random for the first test, and (2) decreased with the order of the test (i.e. due to
 312 habituation). Averaging all aggressiveness scores of an individual in a given year allowed us
 313 to control for these differences and decrease the effect of varying environmental
 314 (meteorological) conditions between tests. In this trivariate model, we included sex and year
 315 as fixed effects and ring number as a random effect. The phenotypic correlation between two
 316 traits A and B , r_{P_A, P_B} , and the between-individual correlation between the traits A and B ,
 317 r_{ind_A, ind_B} , were estimated as follows (Snijders & Bosker 1999):

318
$$r_{P_A, P_B} = \frac{COV_{ind_A, ind_B} + COV_{\epsilon_A, \epsilon_B}}{\sqrt{V_{P_A} \times V_{P_B}}} \quad (1)$$

319
$$r_{ind_A, ind_B} = \frac{COV_{ind_A, ind_B}}{\sqrt{V_{ind_A} \times V_{ind_B}}} \quad (eq. 2)$$

320 where $\text{COV}_{\text{ind}_A, \text{ind}_B}$ and $\text{COV}_{\varepsilon_A, \varepsilon_B}$ are the between- and the within-individual covariances
321 between traits A and B , and $V_{P, A \text{ or } B}$ the total phenotypic variance (sum of the between- and
322 within-individual variances) associated with trait A or B . Combining aggressiveness, boldness
323 and neophobia score data for a given individual in a given year, we obtained 841 observations
324 for which estimates for all three traits were available, and 152 observations for which only
325 boldness and neophobia estimates were available. Among these 841 observations, 49 females
326 and 52 males were repeatedly assessed over several years for all three traits, providing 100
327 and 111 repeated observations, respectively.

328 To estimate the additive genetic correlations between traits, we fitted a model with the
329 same fixed effects but with the additive genetic effect instead of the individual ring as a
330 random factor. Fitting both additive genetic and individual (permanent environment) effects
331 together in a single model indeed led to convergence failures. We thus fitted only one effect at
332 a time.

333

334 *Implementation of Bayesian models*

335 All statistical analyses were performed within the Bayesian framework in R v.3.3.2 (R Core
336 Team, 2016). Both univariate and trivariate models were fitted using the function
337 MCMCglmm ('MCMCglmm' R package, Hadfield, 2010). The pedigree was prepared using
338 the function fixPedigree ('pedantics' R package, Morrissey & Wilson, 2010) and pruned
339 using the function prunePed ('nativ' R package, Wolak, 2012; see Appendix Table A1 for a
340 description of the pedigree). Aggressiveness and boldness scores were fitted with a Poisson
341 family (logit link), and neophobia scores with a Threshold family with the residual variance
342 fixed to 10 (instead of the usual value of 1, to improve the mixing of the chains for low
343 variances, which were expected from preliminary analyses; Hadfield, 2016). We used wide
344 normally distributed priors for fixed effects (large variance $V=10^8$; Hadfield, 2016) and

345 parameter expanded χ^2 distributed priors with 1 degree of freedom for random effects. For the
346 univariate models, we adjusted the number of iterations, burn-in and thinning interval for each
347 model so as to obtain an effective sample size over 1500 (see Appendix) and autocorrelations
348 of posterior samples below 0.1 in all cases. For the trivariate models, we used 4×10^6
349 iterations, a burn-in of 10^5 and a thinning interval of 2000 to reach the same criteria. We
350 visually assessed the convergence of each MCMC chain and compared three chains per model
351 using the Gelman & Rubin approach (`gelman.diag` and `gelman.plot` functions, ‘coda’ R
352 package, Plummer et al., 2016). Following Nakagawa and Schielzeth (2010), we retained in
353 our univariate models data from individuals tested only once. For all three traits, estimates are
354 presented as posterior modes with the associated 95% credible intervals (CI). Variance,
355 repeatability and heritability estimates are presented on the latent scale (R_{latent} , following
356 Nakagawa & Schielzeth, 2010; h^2_{latent} following de Villemereuil, Schielzeth, Nakagawa, &
357 Morrissey, 2016). We also provide repeatability and heritability estimates on the observed
358 scale (R_{obs} using the `QGicc` function, h^2_{obs} using the `QGparams` function, from the ‘`QGglmm`’
359 R package; de Villemereuil, 2018; de Villemereuil, Schielzeth, Nakagawa, & Morrissey,
360 2015). It is not possible here to discuss all results on the observed scale, even though it is the
361 scale of the realized behaviour, that is, where natural selection can act (see de Villemereuil et
362 al., 2016). Indeed, the estimation of R_{obs} for ordinal traits (here the neophobia score) is
363 complex and is not currently implemented in `QGicc`. To allow us to compare estimates
364 between traits on the observed scale, we computed repeatabilities for neophobia using two
365 alternative scores with nonordinal distributions, namely (1) the latency to enter the nestbox in
366 the presence of the novel object for individuals that entered the nestbox ($N=653$, fitted with a
367 Poisson distribution), and (2) whether the individual entered the nestbox in the presence of the
368 novel object ($N=1064$, binary variable fitted with the threshold family). Moreover, the
369 estimation of h^2_{obs} for ordinal traits provides one heritability estimate per level, which in the

370 case of an artificial categorization as here is not biologically relevant (de Villemereuil, 2018).
371 As the heritability estimates on the observed scale were fairly similar between neophobia
372 levels, we compared the range of heritability estimates found for neophobia with the
373 heritability estimates found on the observed scale for aggressiveness and boldness.
374 Correlations are provided on the latent scale.

375

376 *Ethical note*

377 Permission for catching and ringing adults (here 838 yearlings, 1074 older birds) and
378 nestlings (here 9750) with individually numbered aluminium rings was granted every year by
379 the Ringing Centre from the Museum of Natural History in Stockholm (licence nb. 471: M015
380 to B.D.). Adults were caught in the nest, either directly (females during incubation) or using
381 swinging-door traps (both parents during nestling rearing). Traps were set for at most 30 - 60
382 min depending on nestling age (30 min when nestlings were 5 days old or younger), to avoid
383 nestling starvation if parents did not resume feeding during the catching period; traps were
384 checked every 5–10 min, and removed as soon as the adults had been caught. Catching
385 sessions started after 0600 hours to let birds feed and provision nestlings undisturbed for at
386 least 2 h after the night period (sunrise occurs at approximately 0400 hours during spring).
387 Adults were handled for 5 - 10 min and released straight after manipulation or (when catching
388 both parents during nestling feeding) kept until the partner was captured (up to 40 min
389 maximum). For nestling ringing, whole broods were taken directly from the nest and ringed
390 just beside the nestbox (for approximately 10 min); nestlings that were not handled were kept
391 warm using small heating packs. During the aggressiveness tests, we minimized disturbance
392 by approaching the nestbox as quietly as possible and hiding below a camouflage net.
393 Conversely, for the combined boldness/neophobia test, which aimed at measuring (or
394 controlling for) the reaction towards human presence, we on purpose approached the nestbox

395 conspicuously. During the boldness/neophobia test, nestling satiety was checked at the
396 beginning and in between the two parts of the test, and the test was aborted if nestlings were
397 begging too strongly, to avoid any harmful effect of temporarily decreased provisioning by
398 parents. All the manipulations were performed in accordance with the Swedish legislation
399 applying at the time.

400

401

402 **RESULTS**

403

404 *Univariate models*

405 The level of repeatability for aggressiveness was 0.18 on the latent scale and 0.03 on the
406 observed scale (Table 1). In addition, aggressiveness score was repeatable within years
407 ($R_{\text{latent}}=0.22$, 95% CI = [0.18; 0.26]; $R_{\text{obs}}=0.04$, 95% CI = [0.03; 0.06]) and between years
408 (when averaging the aggressiveness score of 1 year; $R_{\text{latent}}=0.26$, 95% CI = [0.11; 0.38];
409 $R_{\text{obs}}=0.11$, 95% CI = [0.04; 0.20]). The level of repeatability for boldness was 0.11 on the
410 latent scale and 0.10 on the observed scale (Table 1). Neophobia was slightly more repeatable
411 than the other traits on the latent scale (Table 1) as well as on the observed scale when
412 estimated from alternative nonordinal measures ($R_{\text{latent}}=0.25$, 95% CI = [0.06; 0.35] and
413 $R_{\text{obs}}=0.14$, 95%CI = [0.04; 0.23] for the latency to enter the nestbox in the presence of the
414 novel object; $R_{\text{latent}}=0.44$, 95% CI = [0.22; 0.67] and $R_{\text{obs}}=0.29$, 95%CI = [0.12; 0.44] for
415 whether the individual entered the nestbox during the test or not). None of the three
416 behavioural scores, however, were heritable (all 95% CI for V_A and h^2 values included zero;
417 Table 1). Permanent environment effects explained 15% of the phenotypic variance in
418 aggressiveness score (95% CI of $V_{\text{PE}} = [0.28; 0.80]$; Appendix Table A2) and parental
419 identities (i.e. maternal and paternal identities summed) explained 25% of the phenotypic

420 variance in neophobia score (95% CI of $V_M + V_F = [0.38; 8.46]$, even though the lower limit of
421 the 95% CI for each parent identity separately was 0: $[0.00; 6.49]$ for V_M and $[0.00; 5.75]$ for
422 V_F). When excluding the maternal (paternal) identity from the model, the paternal (maternal)
423 identity explained 19% (18%) of the phenotypic variance. Fitting the neophobia model
424 without the maternal and paternal identities did not change the heritability estimate, revealing
425 that these effects were not confounded with the additive genetic effect (results not detailed).
426 Observer identity explained 7% of the phenotypic variance for aggressiveness (95% CI of
427 $V_{\text{Observer}} = [0.14; 0.55]$); paternal identity explained 11% of the phenotypic variance for
428 aggressiveness but only when measuring aggressiveness as the first axis of a principal
429 component analysis (see Appendix). All other variances were low (less than 4 % of the
430 phenotypic variance) or not different from zero (Appendix Tables A1, A2 and A3).

431 Males were more aggressive than females, especially among yearlings (interaction
432 sex*age, with yearling males as reference: 95% CI = $[0.44, 0.81]$; Appendix Fig. A1a). In
433 addition, males were slightly shyer (longer latency to enter in the absence of a novel object)
434 and less neophobic (shorter latency in the presence of a novel object) than females (with
435 female as a reference 95% CI = $[-0.12; -0.02]$ and $[-2.78; -1.07]$ respectively; Appendix Fig.
436 A1b), and this did not depend on age (see Appendix Tables A2 and A3 for sex*age
437 interactions). In addition, individuals with larger broods were bolder (95% CI = $[0.002; 0.06]$;
438 Table A3) and less neophobic (95% CI = $[-1.03; -0.37]$; Table A4). Regarding environmental
439 effects, aggressiveness, boldness and neophobia scores depended on the year: individuals
440 were less aggressive and less neophobic in 2011 than 2012 (Appendix Tables A2 and A4),
441 and shyer in 2011 than 2013 (Appendix Table A3). Finally, individuals were more aggressive
442 in the presence of their partner or neighbouring tits attracted by the stimulus, and during the
443 first tests of the sequence (Appendix Table A2).

444

445 *Trivariate model*

446 Aggressiveness and neophobia scores were phenotypically correlated: more aggressive
447 individuals were less neophobic (Table 2, Appendix Fig. A2a). Boldness and neophobia
448 scores were also phenotypically correlated: bolder individuals were less neophobic (Table 2,
449 Appendix Fig. A2b). The corresponding within-individual correlations were negative (Table
450 2). However, there was no phenotypic correlation between boldness and aggressiveness
451 (Table 2; see Appendix Table A5 for the full model output) and none of the between-
452 individual correlations differed from zero (Table 2). When accounting for an additive genetic
453 effect, none of the additive genetic covariances differed from zero (Table 2; see Table A6 for
454 the full model output).

455

456

457 **DISCUSSION**

458

459 In this study, we tested whether three personality traits (aggressiveness, boldness and
460 neophobia) had a genetic basis in a wild population of collared flycatchers and formed
461 (genetically based) behavioural syndromes during breeding, to shed light on constraints in
462 their possible evolution. None of the three traits were heritable and their repeatability
463 estimates were low (0.11–0.39 on the latent scale for all traits; 0.03–0.10 on the observed
464 scale for aggressiveness and boldness; 0.14 and 0.29 on the observed scale for nonordinal
465 measures of neophobia) compared to average estimates previously found for behavioural traits
466 in two meta-analyses (0.37 in Bell et al., 2009; 0.41 in Holtmann et al., 2017), suggesting
467 strong phenotypic plasticity in these traits. The repeatability originated mainly from
468 permanent environment effects for aggressiveness and from parental effects for neophobia. In
469 addition, we found that the three traits showed phenotypic covariance but no between-

470 individual covariance and no additive genetic covariance. The absence of behavioural
471 syndromes among these personality traits may be due either to a lack of statistical power to
472 detect between-individual covariances or to an absence of functional integration of these traits
473 at the individual level and no genetic correlation at the population level.

474

475 *Factors at the origin of behavioural trait repeatability*

476 Our levels of repeatability, estimated both within and between years for aggressiveness score
477 and between years for boldness and neophobia scores, were lower than usually reported for
478 such behaviours: around 0.50 for aggressiveness and exploration, and around 0.40 for
479 antipredator behaviours (Bell et al., 2009). Interestingly, the repeatability level estimated here
480 for aggressiveness score was similar within and between years, contrary to the usual decrease
481 observed when the time interval between recordings increases (Bell et al., 2009; Chervet,
482 Zöttl, Schürch, Taborsky, & Heg, 2011; Dingemanse et al., 2012; Garamszegi et al., 2015;
483 Holtmann et al., 2017; Wuerz & Krüger, 2015; but see David, Auclair, & Cézilly, 2012 for
484 differences between traits). Overall, our lower levels of repeatability, especially on the
485 observed scale, suggest higher plasticity, both within and between years compared to studies
486 on other species.

487 The observed repeatability in aggressiveness score resulted mostly from permanent
488 environment effects, which explained 15% of the phenotypic variance and 72% of the
489 repeatability in aggressiveness score. Here, because we controlled for the identity of the
490 parents, permanent environment effects could be linked to differences in individual condition
491 or experience. Some measures of personality traits have indeed been found to depend on
492 individual condition or experience (reviewed in Stamps & Groothuis, 2010). In our
493 population, condition and experience also affect breeding habitat choice depending on social
494 cues (e.g. Doligez, Danchin, Clobert, & Gustafsson, 1999; Doligez, Pärt, Danchin, Clobert, &

495 Gustafsson, 2004; Kivelä et al., 2014), which could shape individuals' response to the risk of
496 competition for nest sites. Permanent environment effects may also include a dominance
497 effect (Kruuk & Hadfield, 2007; Wilson et al., 2010), which could not be directly modelled
498 here because full- and half-sib links were too rare in our pruned pedigree for running such
499 complex models (Wilson et al., 2010).

500 In turn, the observed repeatability in neophobia resulted mostly from parental
501 identities, which accounted for 25% of the phenotypic variance and 55% of the between-
502 individual variance. Both pre- and postnatal parental effects have been found to affect
503 exploration and neophobia behavioural responses later in life (e.g. nestling provisioning and
504 exploration in birds, Carere, Drent, Koolhaas, & Groothuis, 2005; maternal hormones early in
505 life and neophobia, Spencer & Verhulst, 2007; see the review in Groothuis & Maestriperi,
506 2013). However, parental identities did not explain between-individual differences in
507 aggressiveness and boldness here, contrary to previous findings (e.g. Eising, Muller, &
508 Groothuis, 2006; reviewed in Groothuis & Maestriperi, 2013). These behavioural responses
509 may be more dependent on individual or local environmental conditions, in particular
510 individual competitive ability and neighbour/predator presence or density, at the time of the
511 test(s). To better understand how parental effects shape behavioural responses later in life in
512 our study population, further experiments (e.g. nestling cross-fostering) would be necessary.

513

514 ***Personality traits with no genetic basis***

515 We found no genetic basis for our three personality traits. A meta-analysis on personality
516 traits in wild animal populations estimated an average heritability level of 0.28 for
517 aggressiveness, 0.31 for boldness and 0.58 for exploration-avoidance (including estimates
518 from novel environment and novel object tests; van Oers & Sinn, 2013). The absence of
519 heritability for our personality traits here was not due to a lack of statistical power to detect

520 significant additive genetic variance based on our sample and social pedigree, because based
521 on the same sample with the same pedigree, we obtained positive heritability estimates for
522 tarsus and wing length ($h^2=0.59$, 95% CI = [0.44; 0.69] for tarsus and $h^2=0.30$, 95% CI =
523 [0.11; 0.50] for wing length, while accounting for maternal and permanent environment
524 effects) which are consistent with previous estimates in this population ($h^2 = 0.53$ and 0.51 for
525 tarsus and wing length, respectively, in Merilä & Gustafsson, 1993). The absence of
526 heritability in our personality traits was therefore likely to be the result of very low additive
527 genetic variance combined with large environmental variance as illustrated, for instance, by
528 between-year differences in behavioural scores, which reflected large variations in
529 environmental conditions between the 3 years of our study (see Morinay, Forsman, Kivelä,
530 Gustafsson, & Doligez, 2018 for differences between 2012 and 2013). Large environmental
531 variance could originate from individuals being tested in different environments (including
532 the social context) in different years, because between-year fidelity to the nestbox and/or
533 partner is very low in this population (approximately 6.7% of 240 individuals bred in the
534 same nestbox several years and 1.0% of 214 identified pairs were faithful over several years).
535 This, however, limited the risk of pseudoreplication (Niemelä & Dingemans, 2017).

536 Because we measured personality traits at the nest during breeding, the reaction of the
537 partner may have affected the reaction of the focal bird during a behavioural test, as found
538 here with a higher aggressiveness score when the partner was present. To account for this
539 effect, we could have included the partner's identity and genetic background (i.e. pedigree) as
540 random effects in our models (see Morinay et al., 2018 for an example in the same
541 population; and Wolf, Brodie III, Cheverud, Moore, & Wade, 1998 for so-called indirect
542 genetic effects). However, this could have led to pseudoreplication, because the behavioural
543 score of the partner itself was most of the time also analysed in this dataset (e.g. around 74%
544 of the females and 90% of the males had their partner tested). To keep exploring a response at

545 the individual level (rather than combining behavioural scores at the pair level), a solution
546 could be to fit a bivariate model of the two partners' responses and include both their
547 pedigree, permanent environment and parental effects in the model. This would, however,
548 require a larger data set than used here to reach sufficient statistical power to detect such
549 effects with such complex models. Furthermore, because the focal bird chooses at least partly
550 its partner (like its nest site), partner's effects can also be expected to be at least partly
551 included in the individual's genetic and permanent environment effects. Disentangling such
552 complex effects may require a more balanced sample of faithful and divorced pairs breeding
553 in the same and different sites over several years than observed in our population.

554

555 *No personality syndrome?*

556 Phenotypic correlations were observed between our personality traits, even though they did
557 not constitute behavioural syndromes (i.e. there was no between-individual correlations): less
558 neophobic individuals were more aggressive and bolder. This was in line with previous
559 studies reporting bolder individuals to be more explorative in a novel environment (or less
560 neophobic in a novel object test; e.g. Garamszegi et al., 2009; van Oers, De Jong, Drent, &
561 van Noordwijk, 2004). Conversely, the absence of correlation between aggressiveness and
562 boldness partly contrasts with previous results reporting more aggressive individuals to be
563 bolder, as part of the proactive–reactive axis, in different species (Koolhaas et al., 1999; Sih,
564 Bell, Johnson, et al., 2004) including the collared flycatcher (Garamszegi et al., 2015).

565 The observed phenotypic correlations resulted solely from correlated changes in
566 behaviours between measurements for the same individuals, that is, within-individual
567 correlations. Within-individual correlations could be due to micro-environmental effects (e.g.
568 nestbox environment), to individual effects (e.g. long-term between-year plasticity but short-
569 term within-year behavioural constraints, for instance due to experience) or to correlated

570 measurement errors (Dingemanse & Dochtermann, 2013). Error correlation, however, is more
571 likely to occur between boldness and neophobia scores, which were extracted from the same
572 test and might both be correlated with feeding rate (with birds investing more in nestling
573 provisioning returning more rapidly to their nest in both situations), than between
574 aggressiveness and neophobia scores, which were measured several weeks apart by different
575 persons in different tests. To tease these sources of within-individual correlations apart,
576 aggressiveness, boldness and neophobia scores need to be estimated several times during the
577 same breeding season and possibly the same phase(s) of the reproductive cycle. The limited
578 number of individuals measured several times here (211 observations of 101 individuals),
579 however, is likely to be why we did not detect between-individual covariance (Dingemanse &
580 Dochtermann, 2013 recommended sample sizes of at least 200 individuals tested twice; see
581 also Garamszegi & Herczeg, 2012). Indeed, based on the same sample, we were not able to
582 obtain positive genetic or between-individual covariances between tarsus and wing length,
583 two morphological traits previously reported as genetically correlated in the same population
584 (Merilä & Gustafsson, 1993).

585 Even though our limited statistical power does not allow us to conclude the absence of
586 behavioural syndromes, this absence, if true, would suggest that selective pressures did not
587 yield or maintain a functional integration between the personality traits investigated here. A
588 true absence of behavioural syndromes among the traits we studied could be explained by
589 specific breeding conditions in our population, possibly altering the selective regimes
590 compared to other populations or species. In our population, the high availability of high-
591 quality nest sites (i.e. nestboxes, provided in excess since the early 1980s) may have released
592 joint selective pressures on exploration to find suitable nest sites and aggressiveness to
593 acquire and defend this resource against dominant competitors (in particular tit species) in a
594 natural context. In turn, providing nestboxes probably increased local breeding densities and

595 thereby competition for food resources during the nestling period, especially in a highly
596 synchronous species such as the collared flycatcher. Furthermore, our population is subjected
597 to very low nest predation rates, due to the absence of mustelid species on Gotland (Doligez
598 & Clobert, 2003), which may have released selective pressures on boldness through the
599 decrease in the need to defend the brood. Overall, these specific breeding conditions may
600 have strongly modified the selective regime for personality traits and for a functional
601 integration between them if they are costly.

602 In conclusion, we showed that aggressiveness, boldness and neophobia are repeatable
603 but not heritable traits and do not seem to form behavioural syndromes in our population of
604 collared flycatchers since only phenotypic correlations were observed between neophobia and
605 the other two traits. Our study thus brings insights on the evolutionary potential of these
606 personality traits alone and in interaction with each other during breeding in a wild population
607 experiencing particular breeding conditions (low competition for nest sites, low nest predation
608 rate). To understand the absence of individual covariance between, and heritable variations in,
609 personality traits in our population, a first step would be to investigate the fitness benefits (i.e.
610 reproductive success and survival) associated with each trait and their interactions. Plasticity
611 in the associations between personality traits should be selected for if the fitness costs and
612 benefits of expressing each trait relative to the others depend on the environmental (including
613 social) context (e.g. competition level or predation risk), which remains to be explored for
614 example by experimentally manipulating these environmental conditions.

615

616 **Conflict of interest**

617 We declare no conflict of interest.

618

619 **Acknowledgments**

620 We are grateful to the landowners from Gotland for allowing us to collect data on their
621 properties, to all fieldworkers who collected the data between 2011 and 2013, and to all the
622 students who contributed to the extraction of data from the audio and video recordings and to
623 building the behavioural database. We also thank Ingrid Ahnesjö and Emmanuel Desouhant,
624 and three anonymous referees for their critical comments on the manuscript. J.M. was funded
625 by the Ministère de l'Enseignement Supérieur et de la Recherche (PhD grant), by Uppsala
626 University (PhD grant and Stiftelsen research grant) and by the University of Lyon (IDEX
627 mobility grant). G.D. was funded by the Région Auvergne Rhône-Alpes (PhD and
628 Explora'Doc grants). L.G. was funded by the Swedish Research Council and B.D. by the
629 Centre National pour la Recherche Scientifique.

630

631 **References**

- 632 Bell, A. M. (2007). Future directions in behavioural syndromes research. *Proceedings of the*
633 *Royal Society B: Biological Sciences*, 274(1611), 755–761.
634 <http://doi.org/10.1098/rspb.2006.0199>
- 635 Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a
636 meta-analysis. *Animal Behaviour*, 77(4), 771–783.
637 <http://doi.org/10.1016/j.anbehav.2008.12.022>
- 638 Brommer, J. E. (2013). On between-individual and residual (co)variances in the study of
639 animal personality: Are you willing to take the 'individual gambit'? *Behavioral Ecology*
640 *and Sociobiology*, 67(6), 1027–1032. <http://doi.org/10.1007/s00265-013-1527-4>
- 641 Brommer, J. E., & Class, B. (2017). Phenotypic correlations capture between-individual
642 correlations underlying behavioral syndromes. *Behavioral Ecology and Sociobiology*,
643 71(3). <http://doi.org/10.1007/s00265-017-2278-4>
- 644 Carere, C., Drent, P. J., Koolhaas, J. M., & Groothuis, T. G. G. (2005). Epigenetic effects on

645 personality traits: Early food provisioning and sibling competition. *Behaviour*, 142(9),
646 1329–1355. <http://doi.org/10.1163/156853905774539328>

647 Carere, C., & Maestriperi, D. (2013). *Animal personalities*. Chicago, IL: The University of
648 Chicago Press.

649 Charmantier, A., & Réale, D. (2005). How do misassigned paternities affect the estimation of
650 heritability in the wild? *Molecular Ecology*, 14(9), 2839–2850.
651 <http://doi.org/10.1111/j.1365-294X.2005.02619.x>

652 Chervet, N., Zöttl, M., Schürch, R., Taborsky, M., & Heg, D. (2011). Repeatability and
653 Heritability of Behavioural Types in a Social Cichlid. *International Journal of*
654 *Evolutionary Biology*, 2011, 1–15. <http://doi.org/10.4061/2011/321729>

655 Cote, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010). Personality-dependent
656 dispersal: characterization, ontogeny and consequences for spatially structured
657 populations. *Philosophical Transactions of the Royal Society of London. Series B,*
658 *Biological Sciences*, 365(1560), 4065–4076. <http://doi.org/10.1098/rstb.2010.0176>

659 David, M., Auclair, Y., & Cézilly, F. (2012). Assessing short- and long-term repeatability and
660 stability of personality in captive zebra finches using longitudinal data. *Ethology*,
661 118(10), 932–942. <http://doi.org/10.1111/j.1439-0310.2012.02085.x>

662 de Villemereuil, P. (2018). Quantitative genetic methods depending on the nature of the
663 phenotypic trait. *Annals of the New York Academy of Sciences*, 1422(1), 29–47.
664 <http://doi.org/10.1111/nyas.13571>

665 de Villemereuil, P., Schielzeth, H., Nakagawa, S., & Morrissey, M. (2016). General methods
666 for evolutionary quantitative genetic inference from generalised mixed models. *Genetics*,
667 204(3), 1–30. <http://doi.org/10.1534/genetics.115.186536>

668 Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of
669 avian personalities in a fluctuating environment. *Proceedings of the Royal Society B:*

670 *Biological Sciences*, 271(1541), 847–852. <http://doi.org/10.1098/rspb.2004.2680>

671 Dingemanse, N. J., Both, C., Drent, P. J., van Oers, K., & van Noordwijk, A. J. (2002).
672 Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal*
673 *Behaviour*, 64(6), 929–938. <http://doi.org/10.1006/anbe.2002.2006>

674 Dingemanse, N. J., Bouwman, K. M., van de Pol, M., van Overveld, T., Patrick, S. C.,
675 Matthysen, E., & Quinn, J. L. (2012). Variation in personality and behavioural plasticity
676 across four populations of the great tit *Parus major*. *Journal of Animal Ecology*, 81(1),
677 116–126. <http://doi.org/10.1111/j.1365-2656.2011.01877.x>

678 Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in
679 behaviour: Mixed-effect modelling approaches. *Journal of Animal Ecology*, 82(1), 39–
680 54. <http://doi.org/10.1111/1365-2656.12013>

681 Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction
682 norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution*,
683 25(2), 81–89. <http://doi.org/10.1016/j.tree.2009.07.013>

684 Dingemanse, N. J., & Réale, D. (2005). Natural selection and animal personality. *Behaviour*,
685 142(9/10), 1165–1190. <http://doi.org/10.1163/156853905774539445>

686 Dingemanse, N. J., & Réale, D. (2013). What is the evidence that natural selection maintains
687 variation in animal personalities? In C. Carere & D. Maestripieri (Eds.), *Animal*
688 *personalities* (pp. 201–220). Chicago, IL: The University of Chicago Press.

689 Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R., & Dawnay, N.
690 (2007). Behavioural syndromes differ predictably between 12 populations of three-
691 spined stickleback. *Journal of Animal Ecology*, 76(6), 1128–1138.
692 <http://doi.org/10.1111/j.1365-2656.2007.01284.x>

693 Dochtermann, N. A. (2011). Testing Cheverud’s conjecture for behavioral correlations and
694 behavioral syndromes. *Evolution*, 65(6), 1814–1820. [28](http://doi.org/10.1111/j.1558-</p></div><div data-bbox=)

695 5646.2011.01264.x

696 Dochtermann, N. A., Schwab, T., & Sih, A. (2015). The contribution of additive genetic
697 variation to personality variation: heritability of personality. *Proceedings of the Royal*
698 *Society B: Biological Sciences*, 282(1798), 20142201.
699 <http://doi.org/10.1098/rspb.2014.2201>

700 Doligez, B., & Clobert, J. (2003). Clutch size reduction as a response to increased nest
701 predation rate in the collared flycatcher. *Ecology*, 84(10), 2582–2588.
702 <http://doi.org/10.1890/02-3116>

703 Doligez, B., Danchin, E., Clobert, J., & Gustafsson, L. (1999). The use of conspecific
704 reproductive success for breeding habitat selection in a non-colonial, hole-nesting
705 species, the collared flycatcher. *Journal of Animal Ecology*, 68(6), 1193–1206.
706 <http://doi.org/10.1046/j.1365-2656.1999.00362.x>

707 Doligez, B., Pärt, T., Danchin, E., Clobert, J., & Gustafsson, L. (2004). Availability and use
708 of public information and conspecific density for settlement decisions in the collared
709 flycatcher. *Journal of Animal Ecology*, 41, 75–87.

710 Drent, P. J., Oers, K. v., & Noordwijk, A. J. v. (2003). Realized heritability of personalities in
711 the great tit (*Parus major*). *Proceedings of the Royal Society B: Biological Sciences*,
712 270(1510), 45–51. <http://doi.org/10.1098/rspb.2002.2168>

713 Duckworth, R. A., & Badyaev, A. V. (2007). Coupling of dispersal and aggression facilitates
714 the rapid range expansion of a passerine bird. *Proceedings of the National Academy of*
715 *Sciences of the United States of America*, 104(38), 15017–22.
716 <http://doi.org/10.1073/pnas.0706174104>

717 Duckworth, R. A., & Kruuk, L. E. B. (2009). Evolution of genetic integration between
718 dispersal and colonization ability in a bird. *Evolution*, 63(4), 968–977.
719 <http://doi.org/10.1111/j.1558-5646.2009.00625.x>

720 Eising, C. M., Muller, W., & Groothuis, T. G. . (2006). Avian mothers create different
721 phenotypes by hormone deposition in their eggs. *Biology Letters*, 2(1), 20–22.
722 <http://doi.org/10.1098/rsbl.2005.0391>

723 Evans, S. R., & Gustafsson, L. (2017). Climate change upends selection on ornamentation in a
724 wild bird. *Nature Ecology and Evolution*, 1(2), 1–5. [http://doi.org/10.1038/s41559-016-](http://doi.org/10.1038/s41559-016-0039)
725 0039

726 Falconer, D. S., & Mackay, T. F. C. (1996). *Introduction to quantitative genetics* (4th editio).
727 London, U.K.: Prentice Hall.

728 Firth, J. A., Hadfield, J. D., Santure, A. W., Slate, J., & Sheldon, B. C. (2015). The influence
729 of nonrandom extra-pair paternity on heritability estimates derived from wild pedigrees.
730 *Evolution*, 69(5), 1336–1344. <http://doi.org/10.1111/evo.12649>

731 Garamszegi, L. Z., Eens, M., & Török, J. (2009). Behavioural syndromes and trappability in
732 free-living collared flycatchers, *Ficedula albicollis*. *Animal Behaviour*, 77(4), 803–812.
733 <http://doi.org/10.1016/j.anbehav.2008.12.012>

734 Garamszegi, L. Z., & Herczeg, G. (2012). Behavioural syndromes, syndrome deviation and
735 the within- and between-individual components of phenotypic correlations: When reality
736 does not meet statistics. *Behavioral Ecology and Sociobiology*, 66(12), 1651–1658.
737 <http://doi.org/10.1007/s00265-012-1439-8>

738 Garamszegi, L. Z., Markó, G., & Herczeg, G. (2012). A meta-analysis of correlated
739 behaviours with implications for behavioural syndromes: Mean effect size, publication
740 bias, phylogenetic effects and the role of mediator variables. *Evolutionary Ecology*,
741 26(5), 1213–1235. <http://doi.org/10.1007/s10682-012-9589-8>

742 Garamszegi, L. Z., Markó, G., Szász, E., Zsebők, S., Azcárate, M., Herczeg, G., & Török, J.
743 (2015). Among-year variation in the repeatability, within- and between-individual, and
744 phenotypic correlations of behaviors in a natural population. *Behavioral Ecology and*

745 *Sociobiology*, 69(12). <http://doi.org/10.1007/s00265-015-2012-z>

746 Garamszegi, L. Z., Rosivall, B., Rettenbacher, S., Markó, G., Zsebok, S., Szölloši, E., ...

747 Török, J. (2012). Corticosterone, avoidance of novelty, risk-taking and aggression in a

748 wild bird: no evidence for pleiotropic effects. *Ethology*, 118(7), 621–635.

749 <http://doi.org/10.1111/j.1439-0310.2012.02049.x>

750 Grafen, A. (1984). Natural selection, kin selection and group selection. In J. R. Krebs & N. B.

751 Davies (Eds.), *Behavioural Ecology: an Evolutionary Approach* (pp. 62–84). Oxford,

752 U.K.: Blackwell Science.

753 Greenberg, R., & Mettke-Hofmann, C. (2001). Ecological aspects of neophobia and neophilia

754 in birds. *Current Ornithology*, 16I, 119–178. <http://doi.org/10.1007/978-1-4615-1211-0>

755 Groothuis, T. G. G., & Maestriperi, D. (2013). Parental influence on offspring personality

756 traits in oviparous and placental vertebrates. In C. Carere & D. Maestriperi (Eds.),

757 *Animal personalities: behaviour, physiology, and evolution* (pp. 317–352). Chicago, IL:

758 The University of Chicago Press.

759 Gustafsson, L. (1987). Interspecific competition lowers fitness in collared flycatchers

760 *Ficedula albicollis*: an experimental demonstration. *Ecology*, 68(2), 291–296.

761 Gustafsson, L. (1989). Collared flycatcher. In: I. Newton (ed.): *Lifetime reproduction in birds*

762 (pp. 75-88). London, U.K.: Academic Press.

763 Hadfield, J. D. (2010). MCMC methods for multi-response Generalized Linear Mixed

764 Models: The MCMCglmm R package. *Journal of Statistical Software*, 33(2), 1–22.

765 <http://doi.org/10.1002/ana.22635>

766 Hadfield, J. D. (2016). MCMCglmm course notes. [https://cran.r-](https://cran.r-project.org/web/packages/MCMCglmm/vignettes/CourseNotes.pdf)

767 [project.org/web/packages/MCMCglmm/vignettes/CourseNotes.pdf](https://cran.r-project.org/web/packages/MCMCglmm/vignettes/CourseNotes.pdf)

768 Hadfield, J. D., Nutall, A., Osorio, D., & Owens, I. P. F. (2007). Testing the phenotypic

769 gambit: Phenotypic, genetic and environmental correlations of colour. *Journal of*

770 *Evolutionary Biology*, 20(2), 549–557. <http://doi.org/10.1111/j.1420-9101.2006.01262.x>

771 Hegyi, G., Rosivall, B., & Török, J. (2006). Paternal age and offspring growth: Separating the
772 intrinsic quality of young from rearing effects. *Behavioral Ecology and Sociobiology*,
773 60(5), 672–682. <http://doi.org/10.1007/s00265-006-0211-3>

774 Holtmann, B., Lagisz, M., & Nakagawa, S. (2017). Metabolic rates, and not hormone levels,
775 are a likely mediator of between-individual differences in behaviour: a meta-analysis.
776 *Functional Ecology*, 31(685–696). <http://doi.org/10.1111/1365-2435.12779>

777 Karlsson Green, K., Eroukhmanoff, F., Harris, S., Pettersson, L. B., & Svensson, E. I. (2016).
778 Rapid changes in genetic architecture of behavioural syndromes following colonisation
779 of a novel environment. *Journal of Evolutionary Biology*, 29, 144–152.
780 <http://doi.org/10.1111/jeb.12769>

781 Kivelä, S. M., Seppänen, J.-T., Ovaskainen, O., Doligez, B., Gustafsson, L., Mönkkönen, M.,
782 & Forsman, J. T. (2014). The past and the present in decision-making: the use of
783 conspecific and heterospecific cues in nest site selection. *Ecology*, 95, 3428–3439.
784 <http://doi.org/10.1890/13-2103.1>

785 Koolhaas, J. ., Korte, S. ., De Boer, S. ., Van Der Vegt, B. ., Van Reenen, C. ., Hopster, H., ...
786 Blokhuis, H. . (1999). Coping styles in animals: current status in behavior and stress-
787 physiology. *Neuroscience & Biobehavioral Reviews*, 23(7), 925–935.
788 [http://doi.org/10.1016/S0149-7634\(99\)00026-3](http://doi.org/10.1016/S0149-7634(99)00026-3)

789 Korsten, P., van Overveld, T., Adriaensen, F., & Matthysen, E. (2013). Genetic integration of
790 local dispersal and exploratory behaviour in a wild bird. *Nature Communications*,
791 4(2362). <http://doi.org/10.1038/ncomms3362>

792 Král, M., & Bícík, V. (1989). Intraspecific aggressive responses of male collared flycatchers
793 (*Ficedula albicollis* temm.). *Acta Universitatis Palackianae Olomucensis, Facultas*
794 *Rerum Naturalium, Biologica XXIX*, 96, 107–122.

795 Král, M., & Bícík, V. (1992). Nest defence by the collared flycatcher (*Ficedula albicollis*)
796 against the great tit (*Parus major*). *Folia Zoologica*, 41(3), 263–269.

797 Kruuk, L. E. B., & Hadfield, J. D. (2007). How to separate genetic and environmental causes
798 of similarity between relatives. *Journal of Evolutionary Biology*, 20(5), 1890–1903.
799 <http://doi.org/10.1111/j.1420-9101.2007.01377.x>

800 Lê, S., Josse, J., & Husson, F. (2008). FactoMineR: an R package for multivariate analysis.
801 *Journal of Statistical Software*, 25(1), 1–18.

802 Merilä, J., & Gustafsson, L. (1993). Inheritance of size and shape in a natural population of
803 collared flycatchers, *Ficedula albicollis*. *Journal of Evolutionary Biology*, 6(3), 375–395.
804 <http://doi.org/10.1046/j.1420-9101.1993.6030375.x>

805 Merilä, J., & Sheldon, B. C. (2000). Lifetime Reproductive Success and Heritability in
806 Nature. *The American Naturalist*, 155(3), 301–310. <http://doi.org/10.1086/303330>

807 Morinay, J., Forsman, J. T., Kivelä, S. M., Gustafsson, L., & Doligez, B. (2018).
808 Heterospecific nest site copying behavior in a wild bird: Assessing the influence of
809 genetics and past experience on a joint breeding phenotype. *Frontiers in Ecology and*
810 *Evolution*, 5(January), 1–14. <http://doi.org/10.3389/fevo.2017.00167>

811 Morrissey, M. B., & Wilson, A. J. (2010). Pedantics: an R package for pedigree-based genetic
812 simulation and pedigree manipulation, characterization and viewing. *Molecular Ecology*
813 *Resources*, 10(4), 711–719. <http://doi.org/10.1111/j.1755-0998.2009.02817.x>

814 Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a
815 practical guide for biologists. *Biological Reviews*, 85, 935–956.
816 <http://doi.org/10.1111/j.1469-185X.2010.00141.x>

817 Niemelä, P. T., & Dingemanse, N. J. (2017). Individual versus pseudo-repeatability in
818 behaviour: Lessons from translocation experiments in a wild insect. *Journal of Animal*
819 *Ecology*, 86(5), 1033–1043. <http://doi.org/10.1111/1365-2656.12688>

820 Niemelä, P. T., Lattenkamp, E. Z., & Dingemanse, N. J. (2015). Personality-related survival
821 and sampling bias in wild cricket nymphs. *Behavioral Ecology*, 26(3), 936–946.
822 <http://doi.org/10.1093/beheco/arv036>

823 Petelle, M. B., Martin, J. G. A., & Blumstein, D. T. (2015). Heritability and genetic
824 correlations of personality traits in a wild population of yellow-bellied marmots
825 (*Marmota flaviventris*). *Journal of Evolutionary Biology*, 28(10), 1840–1848.
826 <http://doi.org/10.1111/jeb.12700>

827 Plummer, M., Best, N., Cowles, K., & Vines, K (2006). CODA: Convergence Diagnosis and
828 Output Analysis for MCMC, *R News*, 6, 7-11.

829 Qvarnström, A. (1997). Experimentally increased badge size increases male competition and
830 reduces male parental care in the collared flycatcher. *Proceedings of the Royal Society B:*
831 *Biological Sciences*, 264(1385), 1225–1231. <http://doi.org/10.1098/rspb.1997.0169>

832 R Core Team. (2016). *R: a language and environment for statistical computing*. Vienna,
833 Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.

834 Reale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O.
835 (2010). Personality and the emergence of the pace-of-life syndrome concept at the
836 population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*,
837 365(1560), 4051–4063. <http://doi.org/10.1098/rstb.2010.0208>

838 Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating
839 animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291–318.
840 <http://doi.org/10.1111/j.1469-185X.2007.00010.x>

841 Rosivall, B., Török, J., Hasselquist, D., & Bensch, S. (2004). Brood sex ratio adjustment in
842 collared flycatchers (*Ficedula albicollis*): results differ between populations. *Behavioral*
843 *Ecology and Sociobiology*, 56(4), 346–351. <http://doi.org/10.1007/s00265-004-0796-3>

844 Schuett, W., Tregenza, T., & Dall, S. R. X. (2010). Sexual selection and animal personality.

845 *Biological Reviews*, 85, 217–246. <http://doi.org/10.1111/j.1469-185X.2009.00101.x>

846 Sheldon, B. C., & Ellegren, H. (1999). Sexual selection resulting from extrapair paternity in
847 collared flycatchers. *Animal Behaviour*, 57(2), 285–298.
848 <http://doi.org/10.1006/anbe.1998.0968>

849 Sheldon, B. C., Kruuk, L. E. B., & Merilä, J. (2003). Natural selection and inheritance of
850 breeding time and clutch size in the collared flycatcher. *Evolution*, 57(2), 406–420.
851 <http://doi.org/10.1111/j.0014-3820.2003.tb00274.x>

852 Sih, A., Bell, A. M., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and
853 evolutionary overview. *Trends in Ecology & Evolution*, 19(7), 372–378.
854 <http://doi.org/10.1016/j.tree.2004.04.009>

855 Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: an
856 integrative overview. *The Quarterly Review of Biology*, 79(3), 241–277.
857 <http://doi.org/10.1086/422893>

858 Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of
859 behavioural syndromes. *Ecology Letters*, 15(3), 278–289. <http://doi.org/10.1111/j.1461-0248.2011.01731.x>

860

861 Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-
862 analysis. *Behavioral Ecology*, 19(2), 448–455. <http://doi.org/10.1093/beheco/arm144>

863 Spencer, K. A., & Verhulst, S. (2007). Delayed behavioral effects of postnatal exposure to
864 corticosterone in the zebra finch (*Taeniopygia guttata*). *Hormones and Behavior*, 51(2),
865 273–280. <http://doi.org/10.1016/j.yhbeh.2006.11.001>

866 Stamps, J., & Groothuis, T. G. G. (2010). The development of animal personality: Relevance,
867 concepts and perspectives. *Biological Reviews*, 85(2), 301–325.
868 <http://doi.org/10.1111/j.1469-185X.2009.00103.x>

869 Svensson, L. (1992). *Identification guide to european passerines* (Märstatryc). Stockholm,

870 Sweden: Svensson.

871 van Oers, K., De Jong, G., Drent, P. J., & van Noordwijk, A. J. (2004). A genetic analysis of
872 avian personality traits: Correlated response to artificial selection. *Behavior Genetics*,
873 *34*(6), 611–619. <http://doi.org/10.1007/s10519-004-5588-z>

874 van Oers, K., de Jong, G., van Noordwijk, A. J., & Drent, P. J. (2005). Contribution of
875 genetics to the study of animal personalities: a review of case studies. *Behaviour*, *142*(9),
876 1185–1206. <http://doi.org/10.1163/156853905774539364>

877 van Oers, K., Drent, P. J., de Goede, P., & van Noordwijk, A. J. (2004). Realized heritability
878 and repeatability of risk-taking behaviour in relation to avian personalities. *Proceedings*
879 *of the Royal Society B: Biological Sciences*, *271*, 65–73.
880 <http://doi.org/10.1098/rspb.2002.2168>

881 van Oers, K., & Sinn, D. L. (2011). Towards a basis for the phenotypic gambit: advances in
882 the evolutionary genetics of animal personality. In M. Inoue-Murayama, S. Kawamura,
883 & A. Weiss (Eds.), *From genes to behavior* (pp. 165–183). Tokyo, Japan: Springer.

884 van Oers, K., & Sinn, D. L. (2013). Quantitative and molecular genetics of animal
885 personality. In C. Carere & D. Maestripieri (Eds.), *Animal personalities: behaviour,*
886 *physiology, and evolution* (pp. 149–200). Chicago, IL: The University of Chicago Press.

887 Wilson, A. J., Réale, D., Clements, M. N., Morrissey, M. M., Postma, E., Walling, C. A., ...
888 Nussey, D. H. (2010). An ecologist's guide to the animal model. *Journal of Animal*
889 *Ecology*, *79*(1), 13–26. <http://doi.org/10.1111/j.1365-2656.2009.01639.x>

890 Wolak, M. E. (2012). nadiv: an R package to create relatedness matrices for estimating non-
891 additive genetic variances in animal models. *Methods in Ecology and Evolution*, *3*(5),
892 792–796. <http://doi.org/10.1111/j.2041-210X.2012.00213.x>

893 Wolf, J. B., Brodie III, E. D. B., Cheverud, J. M., Moore, A. J., & Wade, M. J. (1998).
894 Indirect genetic effects. *Trends in Ecology & Evolution*, *13*(2), 64–69.

895 [http://doi.org/10.1016/S0169-5347\(97\)01233-0](http://doi.org/10.1016/S0169-5347(97)01233-0)

896 Wuerz, Y., & Krüger, O. (2015). Personality over ontogeny in zebra finches: Long-term
897 repeatable traits but unstable behavioural syndromes. *Frontiers in Zoology*, 12(1).
898 <http://doi.org/10.1186/1742-9994-12-S1-S9>

899

900 **Appendix**

901 Aggressiveness score

902 We estimated aggressiveness score using the following alternative measures and modelled
903 them using the parameters given in parentheses. (1) Number of aggressive behaviours
904 (movements < 2 m from the nestbox, stationary flights and attacks towards the decoys, chases
905 of live birds) standardized per 15 min (Poisson family; number of iterations = 10^6 ; burn-in =
906 10^4 ; thinning interval = 400). (2) First axis of the PCA presented below (Table A7; Gaussian
907 family; number of iterations = 10^6 ; burn-in = 10^4 ; thinning interval = 400). (3) Discrete score
908 (threshold family, residual variance $V_R = 10$; number of iterations = 13×10^5 ; burn-in = $8 \times$
909 10^4 ; thinning interval = 700). This score was based on the distinction between activity
910 (number of movements/min, including stationary flights and chases) performed far from (> 2
911 m) and close to (< 2 m) the nestbox, and on attacks, subdivided into six categories (Fig. A3a):
912 **0**: individuals that performed no movements (either far from or close to the nestbox); 1:
913 individuals that performed no attack or movements close to the nestbox and performed less
914 than 0.440 movements/min far from (> 5 m) the nestbox; 2: individuals that performed no
915 attack or movements close to the nestbox and performed more than 0.440 movements/min far
916 from (> 5 m) the nestbox; 3: individuals that performed no attacks and less than 0.282
917 movements/min close to (< 2 m) the nestbox; 4: individuals that performed no attacks and
918 between 0.282 and 0.784 movements/min close to (< 2 m) the nestbox; 5: individuals that
919 performed no attacks and above 0.784 movements/min close to (< 2 m) the nestbox; 6:

920 individuals that performed attacks towards decoys(s). The thresholds were chosen so as to
921 distribute individuals equally among categories for scores 1 and 2 on the one hand and scores
922 3, 4 and 5 on the other.

923

924 Boldness score

925 We estimated boldness score using the following alternative measures and modelled them
926 using the parameters given in parentheses. (1) Maximum latency to enter the nestbox after
927 human departure (from all individuals) minus the same latency for the focal individual on the
928 focal test (Poisson family; number of iterations = 1×10^6 ; burn-in = 10^4 ; thinning interval =
929 500). (2) Inverse logarithmic ratio of the latency to enter the nestbox after human departure
930 divided by the feeding rate for the remaining time after the first entrance in the nestbox. We
931 divided by the feeding rate for this alternative measurement because the average feeding
932 interval might have affected the latency to return to the nestbox, for example if individuals
933 feeding more frequently entered the nestbox faster. The feeding rate after the first entrance
934 was estimated as the average time interval between two feeding events by the focal birds,
935 after the first entrance; it was thus only computable for individuals that fed at least twice in
936 the period; for technical reasons, further individuals could not be used for this variable,
937 leading to a final used data set of 641 observations (Gaussian family; number of iterations =
938 25×10^4 ; burn-in = 10^4 ; thinning interval = 100). (3) Discrete score (threshold family, $V_R =$
939 10; number of iterations = 3×10^6 ; burn-in = 2×10^5 ; thinning interval = 1000). The score was
940 based on entrance in the nestbox during the first part of the boldness-neophobia test (no novel
941 object) and latency to enter after human disturbance; individuals that did not enter were given
942 a score of 0, and individuals that entered the nestbox were given a score of 1 - 5 based on five
943 quantiles of the inverse latency to enter (Fig. A3b).

944

945

946 Neophobia score

947 We estimated neophobia score for individuals that entered the nestbox during the first period
948 of the test, using the following alternative measures and modelled them using the parameters
949 given in parentheses. (1) Discrete score based on the latency to enter the nestbox in the
950 presence of a novel object (second period of the test), discretized in four quantiles, the fifth
951 category including individuals that did not enter the nestbox at all in the presence of the novel
952 object (threshold family; $V_R = 10$; number of iterations = 15×10^5 ; burn-in = 2×10^5 ; thinning
953 interval = 500; Fig. A3c); (2) Binary variable separating individuals that did and did not enter
954 during the second period of the test (threshold family; $V_R = 10$; number of iterations = 10^6 ;
955 burn-in = 10^5 ; thinning interval = 500). (3) Latency to enter the nestbox in the presence of the
956 novel object, excluding the individuals that did not enter the nestbox during the second period
957 of the test (Poisson family; number of iterations = 15×10^5 ; burn-in = 15×10^4 ; thinning
958 interval = 500).

959 Results obtained for these alternative scores for the three behavioural traits are given in
960 Tables A2 to A4, and the main text presents the first score in each case.

961 **TABLES**

962

963 **Table 1.** Between-year repeatability and heritability estimates for aggressiveness, boldness
 964 and neophobia scores

	R_{latent}	R_{obs}	h^2_{latent}	h^2_{obs}
Aggressiveness	0.18 *	0.03 *	0.00	0.00
	[0.15; 0.23]	[0.02; 0.04]	[0.00; 0.08]	[0.00; 0.008]
Boldness	0.11 *	0.10 *	0.00	0.00
	[0.01; 0.21]	[0.01; 0.19]	[0.00; 0.10]	[0.00; 0.09]
Neophobia	0.39 *		0.00	0.00 for all scores
	[0.25; 0.54]		[0.00; 0.15]	From [0.00; 0.00] to [0.00; 0.09]

965

966 Repeatabilities and heritabilities (posterior modes and 95% credible intervals) are given on
 967 the latent scale (R_{latent} , h^2_{latent}) and on the observed scale (R_{obs} obtained with the QGicc function
 968 and h^2_{obs} with the QGparams function from ‘QGglmm’ R package; de Villemereuil et al.
 969 2016; de Villemereuil 2018). Asterisks indicate estimates whose 95% CI do not encompass
 970 zero. For aggressiveness, estimates are given using all scores. For neophobia, we provide a
 971 range of heritability values on the observed scale, since one value is provided per neophobia
 972 score level (i.e. five values in total); however, we could not derive repeatability estimates on
 973 the observed scale for ordinal variables.

974

975 **Table 2.** Phenotypic, between- and within-individual, and additive genetic correlations
 976 between aggressiveness, boldness and neophobia scores
 977

	Aggressiveness	Boldness	Aggressiveness
Correlation level	-	-	-
	Neophobia	Neophobia	Boldness
Phenotypic	-0.20*	-0.30*	0.02
	[-0.25; -0.12]	[-0.38; -0.23]	[-0.04; 0.10]
Between-individual	0.00	0.00	-0.02
	[-0.06; 0.06]	[-0.07; 0.05]	[-0.06; 0.06]
Within-individual	-0.28*	-0.43*	0.03
	[-0.38; -0.18]	[-0.53; -0.32]	[-0.04; 0.12]
Additive genetic	0.00	-0.01	0.01
	[-0.06; 0.006]	[-0.06; 0.06]	[-0.07; 0.06]

978
 979 Posterior modes and 95% credible intervals (CI) on the latent scale are shown. Asterisks
 980 indicate estimates whose 95% CI do not encompass zero.

981 **Table A1.** Detailed description of the collared flycatcher pedigree from the Gotland

982 Island population

Pedigree statistics	
Records	2 218
Founders	1423
Maternities	728
Paternities	781
Mothers with ≥ 2 offspring	120
Fathers with ≥ 2 offspring	133
Full sibs	130
Maternal sibs	222
Maternal half sibs	92
Paternal sibs	230
Paternal half sibs	100
Maternal grandmothers	249
Maternal grandfathers	268
Paternal grandmothers	220
Paternal grandfathers	236
Maximum pedigree depth	15
Mean relatedness	5.29×10^{-4}

983

984 The pedigree statistics were obtained from all identified individuals involved in either
985 aggressiveness, boldness or neophobia assays, and were extracted using the pedigreeStats and
986 pedStatSummary functions from ‘pedantics’ R package (Morrissey & Wilson, 2010).

987

1 **Table A2.** Output of the univariate models fitting aggressiveness score

	Number of aggressive behaviours/15 min				PC1		D
	Without fixed effect		With fixed effects				
	Posterior mode	95% CI	Posterior mode	95% CI	Posterior mode	95% CI	
Fixed effects							
Intercept	1.22	[0.91 ; 1.50] *	-0.29	[-0.72 ; 0.26]	-0.98	[-1.30 ; -0.65] *	5
Sex (male)			0.63	[0.44 ; 0.81] *	0.50	[0.35 ; 0.62] *	1
Age (young)			0.23	[-0.01 ; 0.40]	0.06	[-0.05 ; 0.25]	0
Presence of tits (present)			0.34	[0.19 ; 0.50] *	0.05	[-0.07 ; 0.15]	0
Presence of flycatchers (present)			0.27	[-0.02 ; 0.55]	0.29	[0.05 ; 0.49] *	0
Presence of the partner (present)			0.62	[0.44 ; 0.80] *	0.34	[0.20 ; 0.44] *	1
Test number			-0.20	[-0.27 ; -0.14] *	-0.16	[-0.27 ; -0.05] *	-1

							0.20	0.11	
Dummy type (flycatcher)	0.08	[-0.23 ; 0.34]		0.16	[- ; 0.38]		0.01		0
Year (2012)	0.48	[0.08 ; 0.87] *		0.19	[- ; 0.50]		0.05		0
Year (2013)	0.29	[-0.09 ; 0.67]		0.10	[- ; 0.46]		0.09		0
Sex*age (male*young)	0.28	[0.03 ; 0.61] *		0.24	[0.09 ; 0.50] *				0
Random effects									
V_A	0.00	[0.00 ; 0.32]		0.00	[0.00 ; 0.41]		0.00	[0.00 ; 0.16]	0
V_{PE}	0.60	[0.28 ; 0.80] *		0.52	[0.11 ; 0.71] *		0.19	[0.03 ; 0.28] *	1
V_M	0.00	[0.00 ; 0.20]		0.00	[0.00 ; 0.17]		0.00	[0.00 ; 0.12]	0
V_F	0.00	[0.00 ; 0.20]		0.00	[0.00 ; 0.24]		0.23	[0.06 ; 0.37] *	0
V_{plot}	0.07	[0.02 ; 0.16] *		0.05	[0.01 ; 0.15] *		0.01	[0.00 ; 0.04]	0
V_{decoy}	0.00	[0.00 ; 0.03]		0.00	[0.00 ; 0.04]		0.00	[0.00 ; 0.03]	0
V_{song}	0.02	[0.00 ; 0.09]		0.01	[0.00 ; 0.09]		0.00	[0.00 ; 0.03]	0

V_{obs}	0.25	[0.14 ; 0.55] *	0.30	[0.15 ; 0.63] *	0.06	[0.02 ; 0.16] *
V_{ϵ}	2.56	[0.91 ; 1.50] *	2.11	[1.97 ; 2.34] *	1.49	[1.40 ; 1.57] *
Derived estimates						
R_{latent}	0.18	[0.15 ; 0.23] *	0.18	[0.13 ; 0.22] *	0.23	[0.17 ; 0.27] *
R_{obs}	0.03	[0.02 ; 0.04] *	0.03	[0.02 ; 0.04] *	0.21	[0.16 ; 0.25] *
h^2_{latent}	0.00	[0.00 ; 0.08]	0.00	[0.00 ; 0.12]	0.00	[0.00 ; 0.08]
h^2_{obs}	0.00	[0.00 ; 0.01]	0.00	[0.00 ; 0.01]	0.00	[0.00 ; 0.07]
\overline{N}	4680		3271		3271	
Effective sample size	> 2357		> 2234		> 2209	

2

3 Models for the general aggressiveness score, based on the number of aggressive behaviours standardized per 15 min, are shown without and with
4 fixed effects. We also present the posterior modes and 95% credible intervals (CI) of models for alternative aggressiveness scores: the first axis
5 of the principal component analysis (PC1) and the discrete score (see Appendix). Asterisks indicate estimates whose 95% CI do not encompass
6 zero. For categorical fixed terms, estimates refer to the category indicated in parentheses. V_A , V_{PE} , V_M , V_F and V_e refer to the additive genetic,
7 permanent environment, maternal, paternal and residual variances, respectively. V_{plot} , V_{decoy} , V_{song} , V_{obs} refer to the variances associated with the
8 plot, the decoy set used, the song track played and observer identity, respectively. N is the sample size of the data set used in the model.

- 9 Repeatability and heritability estimates are given both on the latent scale ($R_{\text{latent}}, h^2_{\text{latent}}$) and on the observed scale ($R_{\text{obs}}, h^2_{\text{obs}}$) whenever these
- 10 could be estimated.

11 **Table A3 Output of the models fitting boldness scores.**

	Maximum latency–individual latency				Latency/feeding rate		Discrete score
	Without fixed effects		Without fixed effects				
	Posterior mode	95% CI	Posterior mode	95% CI	Posterior mode	95% CI	Posterior mode
Fixed effects							
Intercept	8.00	[7.97 ; 8.04] *	8.05	[7.96 ; 8.10] *	-3.78	[-4.07 ; 3.46] *	4.80
Sex (male)			-0.04	[-0.12 ; 0.02]	-0.10	[-0.29 ; 0.13]	-1.33
Age (young)			-0.02	[-0.10 ; 0.05]	-0.12	[-0.39 ; 0.13]	-0.65
Year (2012)			-0.03	[-0.10 ; 0.04]	0.05	[-0.19 ; 0.43]	-0.38
Year (2013)			0.08	[0.00 ; 0.16] *	0.47	[0.10 ; 0.73] *	1.46
No. of chicks			0.03	[0.00 ; 0.06] *	0.26	[0.15 ; 0.33] *	0.36
Sex*age (male*young)			0.03	[-0.08 ; 0.13]	0.30	[-0.18 ; 0.55]	0.60
Random effects							
V_A	0.00	[0.00 ; 0.02]	0.00	[0.00 ; 0.03]	0.00	[0.00 ; 0.20]	0.01

V_{PE}	0.00	[0.00 ; 0.02]	0.00	[0.00 ; 0.03]	0.00	[0.00 ; 0.25]	0.04
V_M	0.00	[0.00 ; 0.02]	0.00	[0.00 ; 0.02]	0.00	[0.00 ; 0.13]	0.01
V_F	0.00	[0.00 ; 0.01]	0.00	[0.00 ; 0.01]	0.00	[0.00 ; 0.15]	0.01
V_{plot}	0.00	[0.00 ; 0.00]	0.00	[0.00 ; 0.01]	0.00	[0.00 ; 0.07]	0.00
V_{obs}	0.00	[0.00 ; 0.00]	0.00	[0.00 ; 0.00]	0.00	[0.00 ; 0.03]	0.00
V_{ϵ}	0.16	[0.14 ; 0.17] *	0.13	[0.11 ; 0.16] *	1.20	[0.93 ; 1.37] *	10.00
Derived estimates							
R_{latent}	0.11	[0.01 ; 0.21] *	0.19	[0.07 ; 0.31] *	0.12	[0.01 ; 0.29] *	0.28
R_{obs}	0.10	[0.01 ; 0.19] *	0.12	[0.02 ; 0.23] *	0.04	[0.01 ; 0.14] *	
h^2_{latent}	0.00	[0.00 ; 0.10]	0.00	[0.00 ; 0.18]	0.00	[0.00 ; 0.14]	0.00
h^2_{obs}	0.00	[0.00 ; 0.09]	0.00	[0.00 ; 0.09]	0.00	[0.00 ; 0.06]	Posterior m
N		1064		914		641	
						>	
Effective sample size		> 1718		> 1979		2053	

12 Models for the general boldness estimate (maximum latency to enter the nestbox after human disturbance observed in the entire data set minus
13 the individual latency) are shown without and with fixed effects. We also present the posterior modes and 95% credible intervals (CI) of models

14 for alternative boldness estimates: the log-transformed and inverse ratio of the latency to enter the nestbox after human disturbance over the
15 feeding rate during the time remaining and the discrete score based on the latency (see Appendix). Asterisks indicate estimates whose 95% CI do
16 not encompass zero. For categorical fixed terms, estimates refer to the category indicated in parentheses. V_A , V_{PE} , V_M , V_F and V_e refer to the
17 additive genetic, permanent environment, maternal, paternal and residual variances, respectively. V_{plot} and V_{obs} refer to the variances associated
18 with the plot and the observer identity, respectively. N is the sample size of the data set used in the model. Repeatability and heritability estimates
19 are given both on the latent scale (R_{latent} , h^2_{latent}) and on the observed scale (R_{obs} , h^2_{obs}) whenever these could be estimated. Repeatability and
20 heritability estimates for the latency/feeding rate model (fitted with a Gaussian distribution) differ between the latent and observed scales because
21 we accounted for the inverse log transformation in the `QGicc` and `QGparams` functions (`'QGglmm'` R package; de Villemereuil et al. 2016).

22 **Table A4. Output of the models fitting neophobia scores**

	Discrete score				Binary		La
	Without fixed effect		With fixed effects		Posterior mode	95% CI	
	Posterior mode	95% CI	Posterior mode	95% CI			
Fixed effects							
Intercept	4.22	[3.40 ; 4.94] *	5.08	[3.63 ; 6.38] *	-1.67	[-3.39 ; -0.30] *	6.
Sex (male)			-1.89	[-2.78 ; -1.07] *	-1.45	[-2.44 ; -0.41] *	-0.
Age (young)			-0.18	[-1.01 ; 0.76]	0.07	[-1.26 ; 0.92]	-0.
Year (2012)			1.62	[0.72 ; 2.93] *	2.19	[0.59 ; 3.85] *	0.
Year (2013)			1.21	[-0.05 ; 2.37]	1.84	[-0.06 ; 3.34]	0.
Boldness			-1.58	[-1.93 ; -1.12] *	-1.34	[-1.95 ; -0.93] *	-0.

No. of chicks			-0.71	[-1.03 ; -0.37] *	-0.71	[-1.15 ; -0.30] *	-0.71	[-1.15 ; -0.30] *	-0.71
Sex*age (male*young)			-1.02	[-2.44 ; 0.11]	-0.79	[-2.75 ; 0.69]	-0.79	[-2.75 ; 0.69]	-0.79

Random effects

V_A	0.02	[0.00 ; 2.90]	0.03	[0.00 ; 5.76]	0.08	[0.00 ; 8.41]	0.08	[0.00 ; 8.41]	0.08
V_{PE}	0.04	[0.00 ; 5.77]	0.06	[0.00 ; 9.03]	0.05	[0.00 ; 10.70]	0.05	[0.00 ; 10.70]	0.05
V_M	0.04	[0.00 ; 6.49]	0.06	[0.00 ; 8.81]	0.12	[0.00 ; 22.53]	0.12	[0.00 ; 22.53]	0.12
V_F	0.02	[0.00 ; 5.75]	0.03	[0.00 ; 7.85]	0.04	[0.00 ; 11.33]	0.04	[0.00 ; 11.33]	0.04
V_{plot}	0.98	[0.26 ; 2.50] *	1.01	[0.27 ; 3.42] *	0.80	[0.00 ; 3.08]	0.80	[0.00 ; 3.08]	0.80
V_{obs}	0.28	[0.02 ; 1.01] *	0.38	[0.00 ; 1.41]	0.80	[0.14 ; 3.14] *	0.80	[0.14 ; 3.14] *	0.80
V_{ϵ}	10.00	[10.00 ; 10.00]	10.00	[10.00 ; 10.00]	10.00	[10.00 ; 10.00]	10.00	[10.00 ; 10.00]	10.00

Derived estimates

R_{latent}	0.39	[0.25 ; 0.54] *	0.50	[0.33 ; 0.63] *	0.56	[0.35 ; 0.75] *	0.56	[0.35 ; 0.75] *	0.56
R_{obs}					0.29	[0.17 ; 0.48] *	0.29	[0.17 ; 0.48] *	0.29
h^2_{latent}	0.00	[0.00 ; 0.15]	0.00	[0.00 ; 0.22]	0.00	[0.00 ; 0.26]	0.00	[0.00 ; 0.26]	0.00

h^2_{obs}	Posterior mode range: 0.00-0.00	Posterior mode range: 0.00-0.00	0.00	[0.00 ; 0.14]	0.
N	1 064	914	914		
Effective sample size	> 2302	> 2317	> 1583		

23 Models for the general neophobia discrete score, based on the latency to enter the nestbox in presence of the novel object, are shown without and
24 with fixed effects We also present the posterior modes and 95% credible intervals (CI) of models for alternative neophobia estimates: a binary
25 variable (individual entered versus did not enter in the presence of the novel object) and a continuous latency to enter the nestbox, for individuals
26 that entered in the presence of the novel object (see Appendix). Asterisks indicate estimates whose 95% CI do not encompass zero. For
27 categorical fixed terms, estimates refer to the category indicated in parentheses. V_A , V_{PE} , V_M and V_F refer to the additive genetic, permanent
28 environment, maternal and paternal variances, respectively. The residual variance V_ϵ was set to 10. V_{plot} and V_{obs} refer to the variances associated
29 with the plot and the observer identity, respectively. N is the sample size of the data set used in the model. Repeatability and heritability estimates
30 are given both on the latent scale (R_{latent} , h^2_{latent}) and the observed scale (R_{obs} , h^2_{obs}) whenever these could be estimated.

31

32 **Table A5.** Output of the trivariate model fitting aggressiveness, boldness and neophobia scores with an individual random effect

33

	Posterior mode	95% CI	
Fixed effects			
Aggressiveness	1.73	[1.65 ; 1.82]	*
Boldness	7.97	[7.93 ; 8.02]	*
Neophobia	4.44	[3.79 ; 5.00]	*
Sex (male)	-0.02	[-0.06 ; 0.04]	
Year (2012)	0.04	[-0.02 ; 0.09]	
Year (2013)	0.09	[0.03 ; 0.15]	*
Random effects			
$V_{\text{ind, aggressiveness}}$	0.42	[0.16 ; 0.66]	*
$V_{\text{ind, boldness}}$	0.02	[0.00 ; 0.04]	
$V_{\text{ind, neophobia}}$	6.14	[2.96 ; 10.27]	*
$V_{\epsilon, \text{aggressiveness}}$	1.36	[1.09 ; 1.62]	*

$V_{\varepsilon, \text{boldness}}$	0.13	[0.12 ; 0.16]	*
$V_{\varepsilon, \text{neophobia}}$	10.00	[10.00 ; 10.00]	
$\text{COV}_{\text{ind}, \text{aggressiveness-neophobia}}$	0.00	[-0.09 ; 0.11]	
$\text{COV}_{\text{ind}, \text{aggressiveness-boldness}}$	0.00	[-0.01 ; 0.01]	
$\text{COV}_{\text{ind}, \text{boldness-neophobia}}$	0.00	[-0.03 ; 0.02]	
$\text{COV}_{\varepsilon, \text{aggressiveness-neophobia}}$	-1.03	[-1.37 ; -0.63]	*
$\text{COV}_{\varepsilon, \text{aggressiveness-boldness}}$	0.02	[-0.02 ; 0.05]	
$\text{COV}_{\varepsilon, \text{boldness-neophobia}}$	-0.49	[-0.62 ; -0.36]	*
N	1689		
Effective sample size:	>1740		

34

35 V stands for variance terms and Cov for covariance terms (posterior mode and 95% credible interval (CI)). The individual effect was the only
36 random term included; ‘ind’ and ‘ ε ’ stand for between-individual and residual terms, respectively. The residual variance for neophobia score was
37 fixed to 10 (see text for the distributions used for the three scores). Asterisks indicate estimates whose 95% CI do not encompass zero.

38 **Table A6.** Output of the trivariate model fitting aggressiveness, boldness and neophobia scores with an additive genetic effect

39

	Posterior mode	95% CI	
Fixed effects			
Aggressiveness	1.71	[1.62 ; 1.79]	*
Boldness	7.97	[7.93 ; 8.02]	*
Neophobia	4.12	[3.55 ; 4.62]	*
Sex (male)	-0.01	[-0.05 ; 0.04]	
Year (2012)	0.04	[-0.02 ; 0.09]	
Year(2013)	0.09	[0.03 ; 0.15]	*
Random effects			
V_A , aggressiveness	0.15	[0.00 ; 0.38]	
V_A , boldness	0.02	[0.00 ; 0.04]	
V_A , neophobia	4.81	[2.07 ; 7.52]	*
V_ϵ , aggressiveness	1.46	[1.29 ; 1.78]	*

$V_{\epsilon, \text{boldness}}$	0.14	[0.12 ; 0.16]	*
$V_{\epsilon, \text{neophobia}}$	10.00	[10.00 ; 10.00]	
$\text{COV}_A, \text{aggressiveness-neophobia}$	0.00	[-0.06 ; 0.07]	
$\text{COV}_A, \text{aggressiveness-boldness}$	0.00	[0.00 ; 0.00]	
$\text{COV}_A, \text{boldness-neophobia}$	0.00	[-0.02 ; 0.02]	
$\text{COV}_{\epsilon}, \text{aggressiveness-neophobia}$	-1.01	[-1.35 ; -0.64]	*
$\text{COV}_{\epsilon}, \text{aggressiveness-boldness}$	0.01	[-0.02 ; 0.05]	
$\text{COV}_{\epsilon}, \text{boldness-neophobia}$	-0.48	[-0.61 ; -0.37]	*
N	1686		
Effective sample size	> 1816		

40

41 V stands for variance terms and Cov for covariance terms (posterior mode and 95% credible interval (CI)). The additive genetic effect was the
42 only random term included; ‘A’ and ‘ ϵ ’ stand for additive genetic and residual terms, respectively. The residual variance for neophobia score was
43 fixed to 10 (see text for the distributions used for the three scores). Asterisks indicate estimates whose 95% CI do not encompass zero. Positive
44 additive genetic variances are found here because permanent environment and parental effects are not taken into account.

- 1 **Table A7.** Output of a principal component analysis of behaviours recorded during the
- 2 aggressiveness assays

	Coordinates		Contribution	
	PC1	PC2	PC1	PC2
Moves < 2 m from the nestbox	0.83	-0.12	36.12	0.95
Stationary flights towards the decoy	0.73	-0.21	27.74	2.99
Attacks towards the decoy	0.67	-0.24	23.24	4.06
Moves between 2 and 5 m from the nestbox	0.42	0.65	9.40	29.96
Moves between 5 and 10 m from the nestbox	-0.03	0.74	0.03	38.49
Chases of live birds	0.26	0.58	3.47	23.55

3

- 4 We used the function PCA from the ‘FactoMineR’ R package (Lê, Josse, & Husson, 2008).

5 **FIGURE CAPTIONS**

6

7 Figure A1. Sex differences in aggressiveness, boldness and neophobia scores (means \pm 95%
8 confidence interval). (a) Between-sexes differences in average aggressiveness score for a
9 given individual in a given year depending on age (yearling versus older). (b) Between-sexes
10 differences in the latency to return after human disturbance for the period without a novel
11 object, as a proxy of (inverse) boldness, and for the period with the novel object, as a proxy of
12 neophobia. Number of observations is indicated near each estimate.

13

14 Figure A2. (a) Aggressiveness and (b) boldness scores depending on the neophobia score
15 (means \pm 95% confidence interval). See text for the definitions of the scores. Aggressiveness
16 is here the averaged value of all scores for a given individual in a given year. Number of
17 observations is indicated near each estimate.

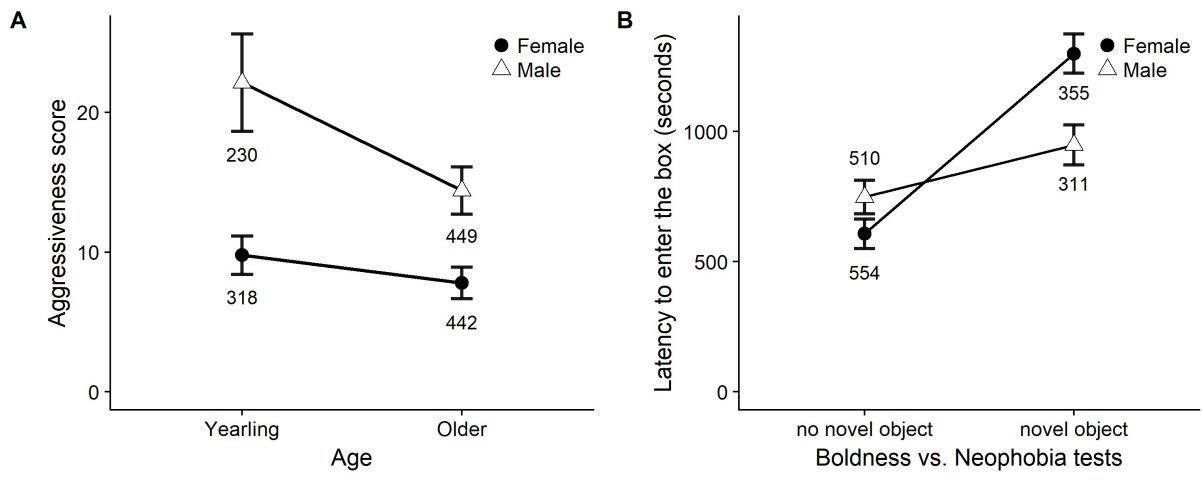
18

19 Figure A3. Distribution of the discrete scores for (a) aggressiveness, (b) boldness and (c)
20 neophobia. Number of observations is indicated above each bar.

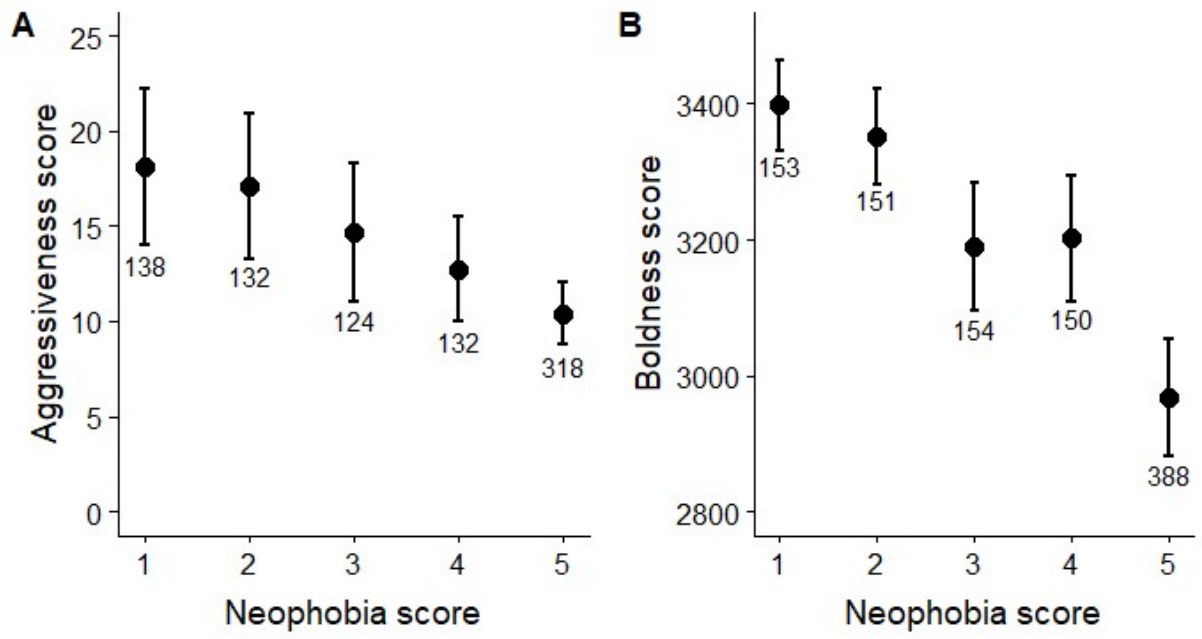
21

22 **Figure A1**

23



24 **Figure A2**



25

26 **Figure A3**

