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

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Abstract

Boldness, defined as the behavioural response of individuals when facing a risky situation, is a major personality trait and often phenotypically correlates with other behavioural traits, in particular aggressiveness, exploration behaviour and neophobia. Yet, whether such links result from among-individual correlations, i.e. form behavioural syndromes *stricto sensu*, is often ignored and whether such syndromes may yield individual fitness benefits, and thus be selected for, remains poorly explored. We measured boldness as the nest defence behaviour against a dummy nest predator in a natural population of a small passerine bird, the collared flycatcher, and investigated the existence of a behavioural syndrome between boldness and two other behavioural traits, aggressiveness (measured as the agonistic response to competitors) and neophobia (measured as the behavioural response to a novel object in a known environment). Then we assessed the links between this potential syndrome and reproductive success, measured as fledging and recruitment success. Boldness score differed between sexes and depended on whether the partner was present during the test. Nevertheless, it was repeatable, showing that boldness can be considered as a personality trait in our population. We found a positive among-individual correlation between boldness and aggressiveness, showing the existence of a behavioural syndrome between both personality traits. This syndrome was related to reproductive success: the number of fledged young (but not recruitment probability) increased with one integrative value of the boldness-aggressiveness syndrome. Conversely, boldness score was not correlated to neophobia. Our results thus clearly reveal a behavioural syndrome between boldness and aggressiveness with possible consequences on reproductive success in the study population, and therefore open up the question of the evolutionary implications of such a behavioural syndrome.

Introduction

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

The interdependence of suites of phenotypic traits has been under recent focus in natural populations, in particular as a mechanism underlying the maintenance of among-individual behavioural differences that are consistent over time and contexts (i.e. repeatable), defined as personality traits (Réale et al., 2007; Dall et al., 2004; Sih et al., 2004; Réale et al., 2010; Wolf & Weissing, 2012), among which boldness. Many studies have indeed reported boldness to be repeatable (Bell et al., 2009). The links now described over many taxa between different personality traits and/or between personality and other phenotypic traits, e.g. physiological and life history traits (Smith & Blumstein, 2008; Réale et al., 2010), have led to the conceptualisation of main behavioural types along a proactive-reactive continuum (Øverli et al., 2007; Toms et al., 2010; Castanheira et al., 2016). Accordingly, boldness has been found to correlate positively with aggressiveness (measured as breeding site or territory defence against competitors) and exploration behaviour (measured as the behavioural response to a novel environment), and negatively with neophobia (measured as the response to a novel object) (Sih & Bell, 2008; Kendall et al., 2018). In a (non-exhaustive) review of the literature on the links between boldness and other behavioural traits, we found a total of 14 studies exploring these links: significant correlations with aggressiveness were reported in 9 studies out of 11, with exploration behaviour in 4 studies out of 5 and with neophobia in 2 studies out of 3 (Appendix Table A1). Such correlations can be modulated by environmental factors (e.g. degree of urbanization: Myers & Hyman, 2016; Ducatez et al., 2017). If boldness positively correlates with aggressiveness and exploration, bold individuals may be more competitive and occupy larger and/or higher quality territories compared to shy ones (e.g. Ward-Fear et al., 2018), as well as locate and access food more quickly (Kurvers et al., 2009, 2012; Dammhahn & Almeling, 2012). Consequently, boldness may be associated with fitness benefits through increased foraging success (Short & Petren, 2008; Patrick & Weimerskirch, 2014; Richardson et al., 2019) as a result from links with other personality traits, outside a risk context. Links with other traits can thus constrain or facilitate the response of boldness to evolutionary pressures.

However, the evolutionary consequences of a phenotypic correlation between traits will depend on whether this correlation results from among-individual rather than common-environment and/or within-individual (or residual) correlation (Sih et al., 2004), i.e. if it represents a behavioural syndrome *stricto sensu* (Dingemanse et al., 2010; Dingemanse & Réale, 2013; Brommer, 2013; Niemelä & Dingemanse, 2018). Very few studies (3 out of the 14 reviewed, to our knowledge; Appendix Table A1) actually explored whether the observed phenotypic correlations between boldness and other traits resulted from among-individual correlations. This was the case in only one study, showing a behavioural syndrome with aggressiveness (Garamszegi et al., 2015). Furthermore, the functional integration of a combination of phenotypic traits, resulting in a behavioural syndrome, will occur only if this syndrome increases fitness, at least in given environmental conditions (Dingemanse et al., 2007). Even though boldness is often found to be linked with measures of individual fitness (8 out of 9 studies in our review: Appendix, Table A1; Smith & Blumstein, 2008), no study to our knowledge investigated the links between syndromes involving boldness and fitness measures (Dingemanse & Réale, 2005, Wolf & Weissing, 2012; but see Bell & Sih, 2007 for a case based on phenotypic correlations). Assessing the fitness consequences of such syndromes thus remains an open question.

In this study, we explored variation in boldness level, measured *in natura* as the nest defence behaviour towards a nest predator, in a breeding population of a small passerine bird, the collared flycatcher *Ficedula albicollis*. In particular, we investigated whether boldness forms a behavioural syndrome with two other behavioural traits, aggressiveness and neophobia, and whether this potential syndrome relates to reproductive success. We first assessed within and between-year repeatability and sources of variation in boldness level against nest predators (including heritability). Previous studies in this species found that boldness measured as the behavioural response towards human presence, as well as aggressiveness and neophobia, were repeatable between years, i.e. can be considered as personality traits (Garamszegi et al., 2009, 2016; Morinay et al., 2019). We therefore expected our boldness score to also reflect a personality trait. Second, we explored the among- and within-individual correlation between boldness and aggressiveness (measured as the agonistic behavioural response towards competitors), and between boldness and neophobia (measured as the response to the presence of a novel object near the nest). Based on results from a meta-analysis (Sih & Bell, 2008; see also Appendix Table A1), we expected phenotypic correlations between these traits, but explored here specifically whether such correlations reflected a behavioural syndrome. Finally, we tested whether a potential syndrome involving boldness was related to reproductive success, measured here by the number of fledged young and recruitment probability, and could thus be under selection. The maintenance of a syndrome can indeed be expected to result from increased fitness benefits of the combination of traits compared to each trait taken independently.

Materials and methods

Study site, study species and population monitoring

Data were collected in a natural population of a small migratory, cavity-nesting passerine bird, the collared flycatcher, breeding on the island of Gotland (Southern Baltic Sea, Sweden; 57°03’N, 18°18’E). Flycatchers arrive on the breeding grounds from late April until late May. Because of strong time constraints, females lay only one clutch, between mid-May and early June (except for rare replacement clutches by pairs that failed very early). In the study area, several hundreds of flycatcher pairs readily breed each year in 1800 nestboxes provided in excess in 20 woodland patches of 2 to 25 ha separated by unsuitable habitat (i.e.

pastures, fields). Since 1980, nestboxes have been regularly visited (at least once a week) each year from May to July to record main breeding data, including laying and hatching dates, clutch size, nestling number and condition and final fledging success. On average, 1/3 of nests fail every year before fledging (between 25 and 50% depending on environmental conditions). Adults breeding in nestboxes have been captured for identification, aging (based on plumage characteristics; Svensson, 1992) and measuring (as well as ringing if previously unringed), during incubation for females and nestling rearing for males. Part of the males are polygynous, providing little care to the young of the secondary female, which often leads to brood failure and the impossibility to catch the male (Gustafsson, 1989). Nestlings were ringed 7 to 12 days posthatching (fledging usually occurs around day 16 posthatching). For more information on the study site and long-term population monitoring, see Pärt & Gustafsson (1989), Doligez et al. (1999, 2004, 2009).

Aggressiveness, neophobia and boldness tests

From 2011 to 2014, three separate behavioural tests were implemented *in natura* on as many pairs as possible in the population, to score the following traits (Réale et al., 2007), in chronological order (Fig. 1): (1) aggressiveness, measured as the agonistic response to a simulated territorial intrusion by intra- or interspecific competitors during the nest building stage; (2) neophobia, measured as the latency to resume nestling feeding in the presence of a novel object on the nestbox during the early nestling stage (i.e. day 5-6 posthatching), and (3) boldness, measured as the risk-taking response to a simulated attack by a nest predator during the late nestling stage (i.e. day 13-14 posthatching). These three tests were thus conducted in different contexts, corresponding to different personality traits: behavioural response in a social context with no or small deadly risk (aggressiveness), response to novelty in a known environment with unknown risk (neophobia) and response to a dangerous situation with known deadly risk (boldness; see Réale et al., 2007, for trait definition). Flycatchers show plumage colour dimorphism allowing an easy distinction between males and females from a distance during behavioural tests.

To measure aggressiveness, we simulated intrusion by a competitor at the time when the risk of losing the box is maximal in this single-clutch species with decoys of either a collared flycatcher pair (intraspecific competitors) or a single great tit (interspecific competitor for nestboxes; Gustafsson, 1987; Forsman et al., 2014). The observer first placed the decoy(s) on the nestbox and then recorded (while hidden) the following behavioural responses by each focal parent: (i) the presence of the bird within four a priori defined distance categories from the nestbox (< 2 m, 2 to 5 m, 5 to 10 m, > 10 m) and all movements within and between these distance categories, (ii) agonistic behaviours towards the stimulus, including attacks and stationary flights in front of the decoy(s), and (iii) chases towards live birds attracted around the nestbox by the stimulus. Recording started immediately after the observer has hidden and continued uninterrupted until the end of the test, whether the bird left the surroundings or not during the test. Tests were performed two to four times depending on field constraints, alternating both stimuli (intra- vs. interspecific), at one day intervals (with one day free from tests in between two series of two tests). For each test, we calculated a behavioural response score following Morinay et al. (2019) by summing the number of (i) movements within the closest zone (i.e. < 2 m) to the nestbox, (ii) agonistic behaviours and (iii) chases, and dividing this sum by the time interval between the first observation of the individual and the end of the test, rescaled to 15 min. For more details, see Fig. 1 and Morinay et al. (2019).

The neophobia test consisted in two consecutive 1-hour long periods during which the behaviour of parents at the nest was video recorded first in the absence of any source of disturbance other than the video recorder (first 1h-period) and second in presence of a novel object (a coloured plastic figurine) placed just beside the nestbox entrance (second 1h-period). This allowed us to compare the time needed to resume nestling feeding with and without the novel object while controlling for human disturbance at the nest and other factors potentially affecting provisioning behaviour such as nestling hunger level. We calculated the neophobia score of each parent as the ratio of the latency (time in s) to resume nestling feeding in presence of the novel object (second period of the test) over the latency to resume feeding in absence of the novel object (first period). To include the individuals that never resumed feeding in presence of the novel object, i.e. the most neophobic ones, we assigned them the maximal latency observed over all tests (i.e. 4000 s here because tests may sometimes last longer than 1 h due to logistical constraints in the field). We excluded from the analyses the few individuals (74 of 1334 observations, i.e. 5.5%) that did not resume feeding without the novel object (first part of the test) because they may have been disturbed by the video recorder. In most cases, both parents returned quickly to the nestbox in the first part of the test (median time of return: 6 min 44 s). For more details, see Fig. 1 and Morinay et al. (2019).

To measure boldness, we simulated an attack by a nest predator to elicit nest defence in response to the risk of losing the brood with a dummy of a red squirrel or great spotted woodpecker (in 2011 only). These predators have been found to occasionally attack flycatcher broods but also parents, and they are often alarmed at and chased by parents when close to the nestbox (Doligez & Clobert, 2003). They represent the main potential nest predators on Gotland where mustelids are absent. The observer first placed the dummy nest predator on the box and then recorded (while hidden) the same behavioural responses of each focal parent than in the aggressiveness test. Again, recording started immediately after the observer was hidden and continued uninterrupted until the end of the test. Tests were performed once or twice on consecutive days depending on field constraints. For each test, we calculated a behavioural response score following Tamin & Doligez (2022) by summing the number of movements within the closest zone (i.e. < 2 m) to the nestbox and attack behaviours (excluding chases), and dividing this sum by the time interval between the first observation of the individual and the end of the test, rescaled to 5 min. We checked whether our results were robust to this boldness score by repeating the analyses using the first principal component of a PCA based on the different behavioural responses recorded during the test as an alternative score (see Appendix and Récapet et al., 2016). For more details, see Fig. 1 and Récapet et al. (2016), Tamin & Doligez (2022).

A previous study in this population quantified a boldness response to human presence at the nestbox (i.e. another potentially dangerous situation associated with known deadly risk) as the latency to return to the nest and resume nestling feeding after a human visit, during the first part of the neophobia test (Morinay et al., 2019). The level of repeatability of this boldness score was however low ($R = 0.11$, 95% CI = [0.01; 0.21]) compared to repeatability usually reported for anti-predator behaviours (on average 0.40; Bell et al., 2009). Using the latency to return to the nest as a score in our nest predator boldness test also yielded a low repeatability level ($R = 0.07$, 95% CI = [0.02; 0.13]) compared to the score described above (see Results). Finally, both latencies were not correlated (Pearson correlation: -0.03 [-0.10; 0.04]). Because the neophobia test was not initially intended to measure boldness in our case and because the risk-taking response in this context may be questioned (individuals actually return after the risk has ended), we thus choose not to use latency here as a boldness score and did not test the link between our boldness score and the score previously described (Morinay et al., 2019; see also Discussion). Including the latency to resume feeding in the first period of the test in the direct computation of our neophobia score also prevented us to use it as a boldness measure here. The total and yearly numbers of individuals tested for each trait is given in Table A2.

Ethical Note

Permission for catching and ringing adults and nestlings (approximatively 4000 individuals between 2011 and 2014) with individually numbered aluminium rings was granted every year by the Ringing Centre of the Museum of Natural History in Stockholm (licence nb. 471:M015 to B.D.). Adult catching and nestling ringing were performed following the methods described in Morinay et al., 2019. During the aggressiveness and boldness tests, we minimized disturbance by approaching the nestbox as quietly as possible and hiding below a camouflage net far away enough not to be detected by individuals. For the neophobia test, we controlled nestling satiety both at the beginning and in between the two parts of the test, and we cancelled the test if nestlings were begging too strongly to avoid potential negative impact of a temporary decrease in parental provisioning due to the presence of the novel object. All the manipulations were performed in accordance with the Swedish legislation applying at the time.

Statistical analyses

Sources of variation in boldness score: univariate GLMMs

We assessed among- and within-individual sources of variation in boldness using a univariate generalized linear mixed model with boldness score as the response variable. The model included as fixed effects individual sex and age (two categories: yearling *vs.* older individual), test order (first or second test for the focal individual, in the cases when two tests were performed in the same year), test date and its squared value (to test for quadratic temporal trends due to differences in the cost/benefit balance of nest defence along the season) and the presence of the partner during the test (which may influence the focal individual's behaviour; Morinay et al., 2019 - see Table A3 for the spelling out of models). Including clutch size as a measure of reproductive investment (previously shown to affect boldness level) or replacing test date by laying date did not change the results (level of repeatability or estimates of other effects, not detailed here). Similarly, including the number of tests the individual has been subjected to in previous years as a measure of its past experience imposed by the test design did not change the results, even though boldness score tended to increase with the number of tests the individual had been subjected to (posterior mode [95% CI]: 0.18 [-0.0003; 0.34]). The model also included as random effects individual identity, observer, dummy identity and the combination of year and woodland patch (to model spatio-temporal environmental variation). We combined patch and year effects here because we were not interested in characterizing spatial and temporal variations separately and to ease model convergence; including them as separate random effects did however not change the results (not detailed here). We obtained 2101 values of boldness score over all tests, with 1.34 tests per individual on average in a given year. We calculated within-year repeatability of boldness score (R) as the individual identity variance ($V_{individual}$) divided by the total phenotypic variance (V_P, sum of all variances; Falconer & Mackay, 1996). Because not all individuals were of known pedigree, we estimated the heritability of boldness using a separate model including the same fixed effects and as random effects the additive genetic effect (associated with the pedigree), maternal and paternal identities, permanent environmental effect (from individual identity once genetic and parental effects have been accounted for), observer, dummy identity and the combination of year and woodland patch. We obtained 671 values of boldness score over all tests with full pedigree information and we calculated boldness score heritability (h^2) as the additive genetic variance (V_A) divided by the total phenotypic variance (V_P; Falconer & Mackay, 1996).

Part of the individuals were measured in several years, thus we also calculated between-year repeatability using another model, with the average value of boldness score over the different tests for a given individual in a given year as the response variable; the model included again sex, age, average test date and its squared value as fixed effects, as well as individual identity and combination of year and patch as random effects (but no additive genetic effect here). We obtained in this case 1384 averaged values of boldness score, with 1.13 tests per individual on average over all years. We calculated between-year repeatability of boldness score (R) as the individual identity variance ($V_{individual}$) divided by the total phenotypic variance (V_P). Although both within- and between-year repeatability could in theory be estimated in a single model by including individual identity and the combination of individual identity with year simultaneously as random effects (Araya-Ajoy et al., 2015), the number of within- and between-year repetitions of boldness scores per individual was too low here to yield a robust model. Thus two separate models had to be used even though this may yield less precise repeatability estimates. Because repeatability estimates may be affected by the presence of fixed factors in the model (Nakagawa & Schielzeth, 2010), we also compared repeatability obtained for the two models (within- and between-year) both with and without fixed effects by checking whether the 95% CI overlapped.

Behavioural syndromes: PCA and bivariate GLMMs

We investigated possible behavioural syndromes between boldness and the two other behavioural traits, aggressiveness and neophobia. These two traits have been found to be repeatable (Morinay et al., 2019; between-year repeatability here based on the slightly modified data set including 2014 data: aggressiveness: N = 1291 individuals, R = 0.26, 95% CI = [0.11; 0.38]; neophobia: N = 852 individuals, R = 0.31, 95% CI = [0.15; 0.48]). We first explored the correlations between the three traits using a principal component analysis on the aggressiveness, boldness and neophobia scores (Cote et al., 2010a). Aggressiveness and boldness scores were averaged over the different tests to obtain a single value for a given individual in a given year; averaging score values is expected to decrease the influence of external factors on behavioural scores (see Morinay et al., 2019). We did not differentiate aggressiveness in response to intra- and inter-specific competition because aggressiveness score did not depend on stimulus type (Morinay et al., 2019). We obtained 688 observations of individuals with a score for the three behavioural traits simultaneously. We used varimax rotation (Quinn & Keough, 2002) and identified principal components with the scree plot and a bootstrapped Kaiser-Guttman (Jackson, 1993); behavioural traits were considered to contribute to principal components when their loading was above 0.32 (Tabachnick & Fidell, 1996).

Second, we used bivariate generalised linear mixed models to partition the phenotypic correlation between boldness and the two other personality traits into among-individual, environmental and within-individual (residual) correlations. We did not implement a single trivariate model on the three traits because this would drastically reduce our sample sizes (40.7% of observations for the boldness and aggressiveness model would be excluded due to missing neophobia score and 15.8% for the boldness and neophobia model due to missing aggressiveness score). Furthermore, the correlation between aggressiveness and neophobia has already been assessed (Morinay et al., 2019). As above, the two bivariate models (boldness-aggressiveness and boldness-neophobia) used average score values (when repeated tests were conducted on the same individual for a given trait in a given year) and included as fixed traits sex, age, average test date and average test date^2 for each trait to account here for possible temporal trends; they also included as random effects individual identity and the combination of year and patch. We did not include an additive genetic effect since none of the three traits were found to be heritable (Morinay et al., 2019 and results below for boldness). Here again, including clutch size or year and patch as separate random effects did not change the results (not detailed here). We obtained 979 observations of individuals with both boldness and aggressiveness scores and 694 with both boldness and neophobia scores. The phenotypic correlation between two behavioural traits A and B, $r_{PA,PB}$, and the among-individual correlation between A and B, $r_{indA,indB}$, were estimated as follows from variances and covariances estimated by the models (Snijders & Bosker, 1999):

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

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

where $Cov_{indA,indB}$, $Cov_{envA,envB}$ and $Cov_{\varepsilon A,\varepsilon B}$ are respectively the among-individual (i.e. individual identity), environmental (i.e. the combination of year and patch) and within-individual (i.e. residual) covariances between traits A and B, and V_{PA} and V_{PB} the total phenotypic variance for traits A and B respectively (sum of the among-individual, common-environment and within-individual variances).

Link between syndrome and reproductive success: univariate GLMMs

To investigate the possible link between reproductive success and a behavioural syndrome involving the traits considered, we first used the value of the first principal component of the PCA on the three traits as an integrative behavioural syndrome score (Cote et al., 2010a; Budaev, 2010; McEvoy et al., 2015). We tested whether this first principal component was linked to the number of fledged young and their local recruitment probability in the following year(s) (i.e. including the juvenile survival phase) using two univariate mixed models. The response variables were either the number of fledged young (from 0 to 8) or local recruitment success (0 if none of the fledged young recruited in the local population, i.e. was captured as an adult, in the following two years or 1 if at least one young recruited; in the sample used here, 105 nests over 380, i.e. 27.6 %, produced at least one recruit). The models included as fixed effects the first principal component, its square value, sex, age, laying date and laying date^2 (to account for the seasonal decrease in reproductive success previously reported in this population: Wiggins et al., 1994), as well as individual identity and the combination of year and patch as random effects. We added the square value of the first principal component to investigate a possible non-linear synergetic effect of the combination of traits involved in a syndrome. Higher relative reproductive benefits could indeed be expected for individuals showing either high or low values of several traits simultaneously, leading to a potential functional integration of these traits.

Because the first principal component of the PCA however explained only part of the between-individual variation in behavioural scores, we also directly investigated the links between reproductive success measures and the behavioural traits involved in the identified syndrome(s) (i.e. with loading > 0.32 on the first principal component) and their interaction as an alternative measure of the syndrome(s). We thus tested whether the interaction between trait scores was linked to the number of fledged young and their local recruitment probability using two new univariate mixed models with the same response variables and fixed and random effects as above, except for the measure of the behavioural syndrome. In addition, we tested whether these trait scores were independently linked to the same measures of reproductive success by including them separately (thus with no interaction) in new univariate models.

Importantly, we did not separate here successful from failed individuals (i.e. based on whether at least one young fledged), as often done to account for a zero-inflated distribution of the number of fledglings, because in our case, nearly all individuals in the sample were successful (i.e. fledged at least one young: 381 out of 385, i.e. 99%). Indeed, the boldness test was performed on pairs that reached the late nestling rearing stage. This automatically excluded most failed pairs from testing both the existence of a behavioural syndrome between boldness and other traits and the link between such a syndrome and reproductive success (see Discussion for potential implications). The number of fledged young was thus normally distributed in this biased sample. Because both parents within a pair shared the same number of fledged and recruited young, we randomly selected the score of one pair member when we had scores for both, to avoid the artificial inflation of reproductive success data due to repeated values within pairs. The random selection was then repeated 100 times to assess the robustness of the links between the measures of behavioural syndrome(s) and reproductive success.

Bayesian procedures

We implemented our analyses within the Bayesian framework in R v3.6.3. Univariate and bivariate (generalised) linear mixed models were run using the MCMCglmm function of the *mcmcglmm* package (Hadfield, 2010) and fitted with a Poisson family (logit link) for aggressiveness, neophobia and boldness scores, a Gaussian family for the number of fledged young and a threshold family (here a binomial family, logit link) for the probability of recruitment. In bivariate models, different test dates were fitted for each response variable using the at.level() function. We implemented the randomisation procedure using the lapply and mclapply functions of the *parallel* package (R Core team, 2022), which provide estimates based on all randomisations combined, thus integrating the uncertainty on the randomly selected data. In all models, we adjusted the number of iterations, burn-in and thinning interval in order to achieve an effective sample size over 2000 and an autocorrelation level of posterior samples below 0.1 in all cases. We used inverse Wishart and expanded priors for all models for both fixed and random effects (univariate models: $V = 1$, $\nu = 1$, $\alpha\mu = 0$, $\alpha V = 1000$; bivariate models: $V = diag(2)$, $\nu = 2$, $\alpha\mu = c(0,0)$, $\alpha V = diag(2)$). We used the Gelman and Rubin approach to assess the convergence of each of three MCMC chains per model (gelman.diag and gelman.plot functions, ‘coda’ R package; Plummer, Best, Cowles & Vines, 2006). All estimates are presented as posterior modes with associated 95% credible intervals (CI) unless otherwise stated.

Results

Sources of variance in boldness score

Boldness score was repeatable both within- and between years, with no major difference when fixed effects were included or not (estimates [95% CI] with *vs.* without fixed effects: within-year: N = 1228 individuals, R = 0.39 [0.31; 0.46] *vs.* N = 1228 individuals, R = 0.40 [0.33; 0.47]; between-years: N = 1204 individuals, R = 0.43 [0.31; 0.58] *vs.* N = 1204 individuals, R = 0.49 [0.32; 0.58]). Using the first principal component of the PCA on all behaviours recorded during the test as an alternative boldness score yielded similar results even though repeatability levels were lower (Appendix Table A4). Boldness was not heritable (h^2 estimate [95% CI] = 0.00 [0.00; 0.20] with fixed effects; 0.00 [0.00; 0.18] without fixed effects; repeatability estimates did not decrease when additive genetic and parental effects were included: Table A5).

Boldness score was higher for males compared to females, as well as when the partner was present during the test compared to when the individual was alone (Table 1). It was also higher in the second test compared to the first when two tests were performed for a given individual in a given year (Table 1). Conversely, boldness score did not depend on age category or test date (Table 1). Again, using the first principal component as an alternative boldness score yielded similar results, except for test date and squared test date, with a score first increasing and then decreasing with test date in this case (Appendix Table A4).

Correlations between boldness, aggressiveness and neophobia scores

In the PCA exploring the correlations between the three behavioural scores, we identified two principal components explaining 75 % of the total variance (Table 2). The first principal component showed high positive loadings (> 0.75) for both boldness and aggressiveness scores while the second principal component showed a high loading (0.95) for the neophobia score alone (Table 2). Thus boldness and aggressiveness scores appeared strongly positively related and independent from the neophobia score.

The bivariate models confirmed this pattern: we observed a positive phenotypic correlation between boldness and aggressiveness scores: more aggressive birds were also bolder (Table 3). This phenotypic correlation resulted from a positive among-individual correlation, while environmental and within-individual correlations did not differ from zero (Table 3). Conversely, boldness and neophobia scores were not phenotypically correlated (Table 3). Thus, boldness and aggressiveness, but not neophobia, form a behavioural syndrome *stricto sensu*. Similar results were obtained when using the first principal component as an alternative boldness score (Appendix Table A6).

Relations between the boldness-aggressiveness syndrome and measures of reproductive success

The first principal component of the PCA between the three behavioural scores used as a measure of the boldness-aggressiveness syndrome was repeatable between years (N = 583 individuals: R = 0.39, 95% CI = [0.04; 0.56]). The number of fledged young increased with the first principal component over the randomisations with one individual per pair randomly selected (posterior mode [95% CI]: 0.30 [0.05; 0.57]; Fig. 2a). Individuals that were simultaneously more aggressive and bolder had a higher fledging success than less aggressive and shyer ones (Fig. 3). The squared value of the first component had no effect on the number of fledged young (posterior mode [95% CI]: -0.05 [-0.15; 0.02]; Fig. 2a). When directly modelling the syndrome with the interaction between aggressiveness and boldness, the number of fledged young was not related to the interaction (posterior mode [95% CI]: 6.33×10^{-5} [-3.28×10^{-4}; 4.58×10^{-4}]; Fig. 2b). In addition, the number of fledged young was linked to neither aggressiveness nor boldness when included separately as fixed effects (posterior mode [95% CI] for aggressiveness: 0.007 [-0.002; 0.015], for boldness: 0.007 [-0.001; 0.015]). None of the other fixed effects were related to the number of fledged young (Appendix Table A7).

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

Discussion

Boldness is a crucial trait shaping responses to risky situations. Yet, the fitness consequences of the frequently observed relations between boldness and other traits remain poorly explored in empirical studies. In a natural population of collared flycatchers, we investigated (i) the sources of variation in boldness measured as nest defence behaviour against a nest predator, (ii) whether boldness is correlated to two other personality traits (aggressiveness and neophobia), forming a behavioural syndrome and (iii) to what extent this syndrome is related to reproductive success, measured here as the number of fledged young and recruitment probability. Besides variation due to individual and environmental factors (sex, presence of the partner during the test), we found that boldness level was repeatable over time both in the short- (within year) and long-term (between years), confirming results of previous studies in many taxa (Réale et al., 2007; Bell et al., 2009) but it was not heritable. A phenotypic correlation was observed between boldness and aggressiveness (but not neophobia) and this correlation resulted from among-individual correlation, revealing a boldness-aggressiveness behavioural syndrome in this population. This boldness-aggressiveness syndrome was linked to our short-term measure of reproductive success, with an increasing number of fledged young when the level of the boldness-aggressiveness syndrome increased, but only when the syndrome was measured by the first principal component of the PCA between the three traits. The syndrome showed no relation with future recruitment probability. Our results may thus suggest fitness consequences of the observed behavioural syndrome, but the resulting constraints on the joint evolution of the traits concerned remain unclear, especially because none of the traits was heritable.

Sources of variation in boldness and behavioural syndrome with aggressiveness

Boldness, measured here as risk-taking behaviour in the context of nest defence, was repeatable over time with a repeatability level similar to those previously reported (Bell et al., 2009). It can thus be considered as a personality trait as in many other populations (e.g. Duckworth, 2006; Kontiainen et al., 2009; Brommer et al., 2014; Fresneau et al., 2014; Garamszegi et al., 2015; Traisnel & Pichegru, 2018). Interestingly, the study population is exposed to a low nest predation pressure due to the absence of mustelids on Gotland. The higher boldness level observed when the partner was present during the test could reflect either (i) a flexible adjustment of risk-taking behaviour depending on the partner's behaviour within a pair or (ii) assortative mating based on boldness. The partner's presence during the test is indeed likely related to its own boldness level, since bolder individuals are more likely to respond to the stimulus and thus be present. In turn, the partner could itself also be more likely to be attracted by a higher nest defence response of the focal individual. Assortative mating with respect to boldness has indeed been reported in different species (e.g. Kortet et al., 2012; Ariyomo & Watt, 2013; Rabdeau et al., 2021) including our study population (Tamin & Doligez, 2022).

Boldness score was here phenotypically positively correlated with aggressiveness score, as previously described in different species (Appendix Table A1). Importantly, this phenotypic correlation resulted from among-individual rather than within-individual (residual) or environmental correlation (here, the year-patch combination). It thus constitutes a behavioural syndrome *stricto sensu* (Dingemanse et al., 2010; Dingemanse & Réale, 2013; Brommer, 2013) between boldness and aggressiveness, which could have potential consequences for the joint evolution of both traits and their fitness consequences (Dingemanse et al., 2004; Sih et al., 2004; Cote et al., 2010b; Karlsson Green et al., 2015). Yet, none of the two traits were heritable (our results and Morinay et al., 2019). Such absence of heritability could result in no constrained evolution for both traits despite the behavioural syndrome described here. In the absence of genetic determinism for the two traits involved, this syndrome could result from early growth conditions shaping the development of behavioural type, which would deserve further investigation. More work is also needed to explore the genetic and non-genetic inheritance of the syndromes themselves and how it may shape their evolution, a question unexplored thus far.

Our results confirm the boldness-aggressiveness syndrome described for collared flycatcher males in another population (Garamszegi et al., 2009, 2016) but they differ from previous results obtained in the same population, with boldness measured in response to human presence (Morinay et al., 2019). Aggressiveness was not correlated (and thus formed no syndrome) with the latency to return to the nest after a visit by a human observer (Morinay et al., 2019). Behavioural response to human presence has been used to measure boldness, for instance through return latency or flight distance, in different species (e.g. Evans et al., 2010, Barnett et al., 2012; Carrillo et al., 2013; Traisnel & Pichegru, 2018), including another population of collared flycatchers (Garamszegi et al., 2015). Yet, individuals have been found to adopt different context-dependent responses depending on the nature of predation risk, i.e. the type of predators (e.g. different responses to ground and aerial predators in relation to nest height: Kleindorfer et al., 2005). The risk associated with humans and nest predators such as those used here is likely to strongly differ for both adults and broods in our study species, as supported by partially different alarm calls in response to these two predator types (T. Tamin and B. Doligez, pers. obs.). In addition, we cannot exclude that individual response was altered here by habituation to human presence due to the frequent visits in the study patches to collect breeding data on this population and on tit populations breeding in nearby nestboxes. Using a boldness score measured in a natural nest predation context, we expect the boldness-aggressiveness syndrome described here to better reflect the result of selective pressures in this population. Boldness measures in response to human perturbations could however be more relevant in an urban ecology context with different sources of risk and associated selective pressures.

Conversely, boldness score was not correlated with neophobia score here. Among personality traits, neophobia is frequently considered as part of the exploration axis (Réale et al., 2007, 2010). Exploration behaviour is usually measured by how an individual interacts with known features when placed in a novel (unknown) environment (Yoshida et al., 2005; Brown et al., 2007; Cote et al., 2010a). In exploration situations in nature, individuals may however be expected to both interact with unknown features and face increased known risks. This may lead to the previously reported correlations between exploration behaviour or neophobia and boldness (Appendix, Table A1). Our result however contrasts with these previous observations and this could suggest that the relation between behavioural responses in the context of unknown (exploration behaviour / neophobia) *vs.* known (boldness) risk may be context-dependent. Our neophobia test here may have involved different direct costs for adults in terms of energy or missed foraging opportunities compared to when neophobia is measured using new objects placed near food resources or new food resources. Responses to different behavioural tests under known or unknown risk could rely on different mechanisms linked to metabolic rate and energy mobilisation, possibly regulating the general proactive-reactive continuum. This could explain the absence of a general behavioural syndrome involving neophobia in our case, while boldness and aggressiveness are linked, but this remains to be explored.

Fitness consequences of the boldness-aggressiveness syndrome

The correlation between boldness and aggressiveness is among the most widely studied behavioural correlations in the wild (see review in Sih & Bell, 2008). Although very few studies directly investigated whether this phenotypic correlation resulted from among-individual correlation, it may reflect a widespread behavioural syndrome (see Brommer & Class, 2017). This suggests that certain combinations of boldness and aggressiveness levels allow individuals to achieve higher reproductive success and/or survival compared to when displaying a given level of each trait separately. Such combinations would thus be favoured by natural selection, leading to a functional integration between both traits (Duckworth et al., 2009; Dingemanse & Réale, 2005; Wolf & Weissing, 2012). Both boldness and aggressiveness have independently been shown to affect fitness (for boldness, see Table S1; for aggressiveness: see e.g. Ariyomo & Watt, 2012; Betini & Norris, 2012) but the links between a boldness-aggressiveness syndrome and fitness components, in particular reproductive success, remained unexplored thus far. Bold individuals were previously found to achieve higher reproductive success compared to shy individuals (Appendix Table A1; Smith & Blumstein, 2008) and this was suggested to result from higher foraging success (Short & Petren, 2008; but see Barnett et al., 2012). If high aggressiveness requires more energy to face agonistic confrontations with competitors, high boldness may allow individuals to sustain this increased demand, and thereby secure a better access to higher quality resources, including breeding territory / site, at the end of competitive processes. In turn, access to high quality resources through increased aggressiveness may facilitate the exploitation of these resources by bold individuals, in a positive feedback loop. Such mechanisms may explain how an aggressiveness-boldness syndrome could provide fitness benefits beyond the mere effects of the two traits separately.

The boldness-aggressiveness syndrome found here was potentially under selection since our combined measure of both traits (the first principal component of the PCA with the three behavioural traits under study, as used by previous studies: Cote et al., 2010a; Budaev, 2010; McEvoy et al., 2015) was linked with short-term reproductive success (i.e. at fledging). Interestingly, this link was observed here in the quasi-absence of nest predation in this population (Doligez & Clobert, 2003), showing that it was not directly due to lower nest predation rate via increased nest defence, but should indeed result from other potential benefits of the two behavioural traits combined. Yet, when the syndrome was measured using the direct interaction between the two traits, no such link was found anymore. The origin of this difference between these two measures of our syndrome is unclear at this stage, but it calls for caution when predicting the selection consequences of the link with this fitness component. While the first principal component leaves much among-individual behavioural variation unexplained, modelling the syndrome with a simple interaction between both traits may not capture the complex synergetic effects of the traits. Furthermore, the structuration of the syndrome was straightforward here (two main traits involved) but with more than two traits involved, interpreting both principal component axes and high-level interactions may be difficult. Building standard operational scores to quantitatively estimate behavioural syndromes allowing us to investigate their fitness consequences remains a challenge for future studies. Furthermore, possible links between our aggressiveness-boldness syndrome and reproductive success could also be indirect, via the simultaneous effect of a third variable on both the expression of the syndrome and reproductive success, such as individual motivation or condition. Future work is thus needed to unravel the exact causal mechanisms leading to possible fitness benefits and thus underlying potential selection for the aggressiveness-boldness syndrome in this and other populations, even though this syndrome should not respond to selection here because the traits involved are not heritable.

Importantly, the sample on which boldness and thus the behavioural syndrome was measured was biased towards successful pairs, i.e. pairs that reached the late (13 days old) nestling stage, because of the practical implementation (timing) of behavioural tests in the field. This may reduce the variation observed in the syndrome level in relation with reproductive success, and thereby reduce our ability to detect such a link with success (for personality-based sampling bias, see Biro & Dingemanse, 2009, Garamszegi et al., 2009). Whether selection on the observed syndrome may translate into longer term evolution should depend on (i) the extent to which the traits concerned are (both genetically and non-genetically) transmitted to offspring but also (ii) the link with other fitness components, in particular survival, including offspring survival until recruitment. Here, we found no link between the boldness-aggressiveness syndrome and local recruitment probability, thus we cannot exclude compensation of lower fledgling success for less aggressive and shyer parents via higher juvenile survival after fledging, leading to no overall link between syndrome and long-term reproductive success. Yet, even under such compensations, differential effects on different fitness components may still have evolutionary consequences. Boldness and aggressiveness may be linked to fitness through different ways: aggressiveness could favour individual settlement and mating through competition for high quality nest sites (flycatchers do usually not defend an all-purpose territory but only the immediate surroundings of a breeding site; Cramp & Perrins, 1993), while boldness may be more generally associated to foraging ability (e.g. Short & Petren, 2008) as well as defense under predator threats (Kleindorfer et al., 2005), and thus survival. Assessing the synergetic impact of boldness and aggressiveness for behavioural syndrome evolution will thus require a thorough investigation of different fitness components and ultimately lifetime reproductive success. Importantly, selection may operate on the ability to jointly adjust the behavioural traits displayed in a syndrome to maximise fitness given individual and environmental conditions, i.e. on joint phenotypic plasticity for boldness and aggressiveness here, rather than on the syndrome itself. Even though each trait was not heritable separately in our case, which prevents the syndrome to directly respond to selection, whether the joint plasticity in the expression of the traits is heritable is currently unknown (see Henriksen et al., 2020). More work will be needed to fully apprehend the long-term fitness consequences of the boldness-aggressiveness syndrome described here and its plasticity, and thereby understand the mechanisms underlying its evolutionary consequences in natural populations.

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Conflict of interest

The authors declare no competing interests.

References

Araya-Ajoy, Y. G., Mathot, K. J., & Dingemanse N. J. (2015). An approach to estimate short-term, long-term and reaction norm repeatability. *Methods in Ecology and Evolution*, *6*, 1462-1473. https://doi.org/10.1111/2041-210X.12430

Ariyomo, T. O., & Watt, P. J. (2012). The effect of variation in boldness and aggressiveness on the reproductive success of zebrafish. *Animal Behaviour*, *83*, 41-46. https://doi.org/10.1016/j.anbehav.2011.10.004.

Ariyomo, T. O., & Watt, P. J. (2013). Disassortative mating for boldness decreases reproductive success in the guppy. *Behavioral Ecology*, *24*, 1320-1326. https://doi.org/10.1093/beheco/art070.

Barnett, C. A., Thompson, C. F., & Sakaluk, S. K. (2012). Aggressiveness, Boldness and Parental Food Provisioning in Male House Wrens (*Troglodytes aedon*). *Ethology*, *118*, 984-993. https://doi.org/10.1111/j.1439-0310.2012.02092.x.

Bell, A. M. (2004). Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*): Behavioural syndromes. *Journal of Evolutionary Biology*, *18*, 464-473. https://doi.org/10.1111/j.1420-9101.2004.00817.x.

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. *Animal Behaviour*, *77*, 771-783. https://doi.org/10.1016/j.anbehav.2008.12.022.

Betini, G. S., & Norris, D. R. (2012). The relationship between personality and plasticity in tree swallow aggression and the consequences for reproductive success. *Animal Behaviour*, *83*, 137-143. https://doi.org/10.1016/j.anbehav.2011.10.018.

Biro, A., & Dingemanse, N. (2009). Sampling bias resulting from animal personality. *Trends in Ecology & Evolution*, *24*, 66-67. https://doi.org/10.1016/j.tree.2008.11.001.

Bourne, G., & Sammons, A. (2008). Boldness, aggression and exploration: evidence for a behavioural syndrome in male pentamorphic livebearing fish, *Poecilia parae*. *Aquaculture, Aquarium, Conservation & Legislation*, *1*, 39-49.

Brommer, J. E., & Class, B. (2017). Phenotypic correlations capture between-individual correlations underlying behavioral syndromes. *Behavioral Ecology and Sociobiology*, *71*, 1-8. https://doi.org/10.1007/s00265-017-2278-4.

Brommer, J. E., Karell, P., Ahola, K., & Karstinen, T. (2014). Residual correlations, and not individual properties, determine a nest defense boldness syndrome. *Behavioral Ecology*, *25*, 802-812. https://doi.org/10.1093/beheco/aru057.

Brommer, J. E. (2013). On between-individual and residual (co) variances in the study of animal personality: are you willing to take the "individual gambit"? *Behavioral Ecology and Sociobiology*, *67*, 1027-1032. https://doi.org/10.1007/s00265-013-1527-4.

Brown, C., Burgess, F., & Braithwaite, V. A. (2007). Heritable and experiential effects on boldness in a tropical poeciliid. *Behavioral Ecology and Sociobiology*, *62*, 237-243. https://doi.org/10.1007/s00265-007-0458-3.

Bubac, C.M., Coltman, D.W., Don Bowen, W. et al. (2018). Repeatability and reproductive consequences of boldness in female gray seals. *Behavioral Ecology and Sociobiology* *72***,** 1-12. https://doi.org/10.1007/s00265-018-2515-5.

Budaev, S. V. (2010). Using principal components and factor analysis in animal behaviour research: caveats and guidelines. *Ethology*, *116*, 472-480. https://doi.org/10.1111/j.1439-0310.2010.01758.x.

Caramujo, M.-J., Crispim, M. C., & Boavida, M.-J. (1997). Assessment of the importance of fish predation versus copepod predation on life history traits of *Daphnia hyalina*. In A. Brancelj, L. Meester, & P. Spaak (Eds.), *Cladocera*: *The Biology of Model Organisms* (pp. 243-252). Springer Dordrecht. https://doi.org/10.1007/978-94-011-4964-8_27.

Careau, V., Thomas, D., Humphries, M. M., & Reale, D. (2008). Energy metabolism and animal personality. *Oikos, 117*, 641-653. https://doi.org/10.1111/j.2008. 0030-1299.16513.x.

Carrillo, J., & Aparicio, J. M. (2001). Nest defence behaviour of the Eurasian kestrel (*Falco tinnunculus*) against human predators. *Ethology*, *107*, 865-875. https://doi.org/10.1046/j.1439-0310.2001.00718.x.

Carrillo, J., & González-Dávila, E. (2013). Aggressive behaviour and nest-site defence during the breeding season in an island kestrel population. *Journal of Ethology*, *31*, 211-218. https://doi.org/10.1007/s10164-013-0369-x.

Castanheira, M. F., Cerqueira, M., Millot, S., Gonçalves, R. A., Oliveira, C. C. V., Conceição, L. E. C., & Martins, C. I. M. (2016). Are personality traits consistent in fish? The influence of social context. *Applied Animal Behaviour Science*, *178*, 96-101. https://doi.org/10.1016/j.applanim.2016.02.004.

Claireaux, M., Jorgensen, & C., Enberg, K. (2018). Evolutionary effects of fishing gear on foraging behaviour and life history traits. *Ecology and Evolution*, *8*, 10711-10721. https:// 10.1002/ece3.4482.

Collins, S. M., Hatch, S. A., Elliott, K. H., & Jacobs, S. R. (2019). Boldness, mate choice and reproductive success in *Rissa tridactyla*. *Animal Behaviour*, *154*, 67-74. https://doi.org/10.1016/j.anbehav.2019.06.007.

Cote, J., Fogarty, S., Weinersmith, K., Brodin, T., & Sih, A. (2010a). Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proceedings of the Royal Society B: Biological Sciences*, *277*, 1571-1579. https://doi.org/10.1098/rspb.2009.2128.

Cote, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010b). Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B*, *365*, 4065-4076. https://doi.org/10.1098/rstb.2010.0176.

Cramp, S. & Perrins, C. M. 1993. *The birds of the Western Palearctic*. Oxford University Press, Oxford.

Curio, E., Regelmann, K., & Zimmermann, U. (1984). The Defence of First and Second Broods by Great Tit (*Parus major*) Parents: A Test of Predictive Sociobiology. *Zeitschrift für Tierpsychologie*, *66*, 101-127. https://doi.org/10.1111/j.1439-0310.1984.tb01359.x.

Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters*, *7*, 734-739. https://doi.org/10.1111/j.1461-0248.2004.00618.x.

Dammhahn, M., & Almeling, L (2012). Is risk taking during foraging a personality trait? A field test for cross-context consistency in boldness. *Animal Behaviour*, *84*, 1131-1139. https://doi.org/ 10.1016/j.anbehav.2012.08.014.

Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*, 847-852. https://doi.org/10.1098/rspb.2004.2680.

Dingemanse, N. J., & Réale, D. (2005). Natural selection and animal personality. *Behaviour*, *142*, 1159-1184. https://doi.org/10.1163/156853905774539445.

Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: Animal personality meets individual plasticity. *Trends in Ecology & Evolution*, *25*, 81-89. https://doi.org/10.1016/j.tree.2009.07.013.

Dingemanse, N. J., & Réale, D. (2013). What is the evidence that natural selection maintains variation in animal personalities? In C. Carere, & D. Maestripieri (Eds.), *Animal Personalities: Behavior, Physiology and Evolution* (pp. 201-220). University of Chicago Press. https://doi.org/10.7208/9780226922065-009.

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

Doligez, B., Danchin, E., Clobert, J., & Gustafsson, L. (1999). The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. *Journal of animal ecology*, *68*, 1193-1206. https://doi.org/10.1046/j.1365-2656.1999.00362.x.

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

Doligez, B., Pärt, T., & Danchin, E. (2004). Prospecting in the collared flycatcher: Gathering public information for future breeding habitat selection? *Animal Behaviour*, *67*, 457-466. https://doi.org/10.1016/j.anbehav.2003.03.010.

Doligez, B., Gustafsson, L., & Pärt, T. (2009). 'Heritability' of dispersal propensity in a patchy population. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 2829-2836. https://doi.org/10.1098/rspb.2009.0454.

Ducatez, S., Audet, J.-N., Rodriguez, J. R., Kayello, L., & Lefebvre, L. (2017). Innovativeness and the effects of urbanization on risk-taking behaviors in wild Barbados birds. *Animal Cognition*, *20*, 33-42. https://doi.org/10.1007/s10071-016-1007-0.

Duckworth, R. A. (2006). Behavioural correlations across breeding contexts provide a mechanism for a cost of aggression. *Behavioral Ecology, 17,* 1011-1019. https://doi.org/10.1093/beheco/arl035.

Duckworth, R. A. (2009). The role of behavior in evolution: a search for mechanism. *Evolutionary ecology*, *23*, 513-531. https://doi.org/10.1007/s10682-008-9252-6.

Edwards, H. A., Burke, T., & Dugdale, H. L. (2017). Repeatable and heritable behavioural variation in a wild cooperative breeder. *Behavioral Ecology*, *28*, 668-676. https://doi.org/10.1093/beheco/arx013.

Evans, J., Boudreau, K., & Hyman, J. (2010). Behavioural Syndromes in Urban and Rural Populations of Song Sparrows. *Ethology*, *116*, 588-595. https://doi.org/10.1111/j.1439-0310.2010.01771.x.

Falconer, D. S., & Mackay, T. E. C. (1996). *Introduction to Quantitative Genetics*. Pearson Education India.

Fresneau, N., Kluen, E., & Brommer, J. E. (2014). A sex-specific behavioral syndrome in a wild passerine. *Behavioral Ecology*, *25*, 359-367. https://doi.org/10.1093/beheco/aru008.

Forsman, J. T., Kivelä, S. M., Jaakkonen, T., Seppänen, J.-T., Gustafsson, L., & Doligez, B. (2014). Avoiding perceived past resource use of potential competitors affects niche dynamics in a bird community. *BMC Evolutionary Biology*, *14*, 1-11. https://doi.org/10.1186/s12862-014-0175-2.

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

Garamszegi, L. Z., Markó, G., Szász, E., Zsebők, S., Azcárate, M., Herczeg, G., & Török, J. (2015). Among-year variation in the repeatability, within- and between-individual, and phenotypic correlations of behaviors in a natural population. *Behavioral Ecology and Sociobiology*, *69*, 2005-2017. https://doi.org/10.1007/s00265-015-2012-z.

Garamszegi, L. Z. (2016). A simple statistical guide for the analysis of behaviour when data are constrained due to practical or ethical reasons. *Animal Behaviour*, *120*, 223-234. https://doi.org/10.1016/j.anbehav.2015.11.009.

Gustafsson, L. (1987). Interspecific competition lowers fitness in collared flycatchers *Ficedula albicollis*: an experimental demonstration. *Ecology*, *68*, 291-296. https://doi.org/10.2307/1939260.

Gustafsson, L. (1989). Collared flycatcher. In I. Newton (Ed.), *Lifetime reproduction in birds* (pp. 75-88). Academic Press.

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, *33*, 1–22. https://doi.org/10.1002/ana.22635.

Harris, S., Ramnarine, I. W., Smith, H. G., & Pettersson, L. B. (2010). Picking personalities apart: estimating the influence of predation, sex and body size on boldness in the guppy *Poecilia reticulata*. *Oikos*, *119*, 1711-1718. https://doi.org/10.1111/j.1600-0706.2010.18028.x.

Henriksen, R., Höglund, A., Fogelholm, J., Abbey-Lee, R., Johnsson, M., Dingemanse, N. J., & Wright, D. (2020). Intra-individual behavioural variability: a trait under genetic control. *International Journal of Molecular Sciences, 21,* 8069. https://doi.org/10.3390/ijms21218069.

Hollander, F. A., Van Overveld, T., Tokka, I., & Matthysen, E. (2008). Personality and Nest Defence in the Great Tit (*Parus major*). *Ethology*, *114*, 405-412. https://doi.org/10.1111/j.1439-0310.2008.01488.x.

Huntingford, F. A. (1976). The relationship betwe en anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus Aculeatus*. *Animal Behaviour*, *24*, 245-260. https://doi.org/10.1016/S0003-3472(76)80034-6.

Jackson, D. A. (1993). Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. *Ecology*, *74*, 2204-2214. https://doi.org/10.2307/1939574.

Karlsson Green, K., F. Eroukhmanoff, S. Harris, L. B. Pettersson, & E. I. Svensson. (2015). Rapid changes in genetic architecture of behavioural syndromes following colonisation of a novel environment. *Journal of Evolutionary Biology*, *29*, 144-152. https://doi.org/10.1111/jeb.12769.

Kendall, B. E., Fox, G. A., & Stover, J. P. (2018). Boldness-aggression syndromes can reduce population density: Behavior and demographic heterogeneity. *Behavioral Ecology*, *29*, 31-41. https://doi.org/10.1093/beheco/arx068.

King, A. J., Fürtbauer, I., Mamuneas, D., James, C., & Manica, A. (2013). Sex-Differences and Temporal Consistency in Stickleback Fish Boldness. *PLoS ONE*, *8*, e81116. https://doi.org/10.1371/journal.pone.0081116.

Kleindorfer, S., Fessl, B., & Hoi, H. (2005). Avian nest defence behaviour: Assessment in relation to predator distance and type, and nest height. *Animal Behaviour*, *69*, 307-313. https://doi.org/10.1016/j.anbehav.2004.06.003.

Kortet, R., Niemelä, P. T., Vainikka, A., & Laakso, J. (2012). Females Prefer Bold Males; an Analysis of Boldness, Mate Choice, and Bacterial Resistance in the Field Cricket *Gryllus integer*. *Ecological Parasitology and Immunology*, *1*, 1-6. https://doi.org/10.4303/epi/235580.

Kluen, E., Siitari, H., & Brommer, J. E. (2014). Testing for between individual correlations of personality and physiological traits in a wild bird. *Behavioral Ecology and Sociobiology*, *68*, 205-213. https://doi.org/10.1007/s00265-013-1635-1.

Kontiainen, P., Pietiäinen, H., Huttunen, K., Karell, P., Kolunen, H., & Brommer, J. E. (2009). Aggressive Ural owl mothers recruit more offspring. *Behavioral Ecology*, *20*, 789-796. https://doi.org/10.1093/beheco/arp062.

Kurvers, R. H. J. M., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S.E., Ydenberg R.C. et al. (2009). Personality differences explain leadership in barnacle geese. *Animal Behaviour*, *78*, 447-453. https://doi.org/10.1016/j.anbehav.2009.06.002.

Kurvers, R. H. J. M., Nolet, B. A., Prins, H. H. T., Ydenberg, R. C., & van Oers, K. (2012). Boldness affects foraging decisions in barnacle geese: An experimental approach. *Behavioral Ecology*, *23*, 1155-1161. https://doi.org/10.1093/beheco/ars091.

Lucon-Xiccato, T., Montalbano, G., & Bertolucci, C. (2020). Personality traits covary with individual differences in inhibitory abilities in two species of fish. *Current Zoology*, *66*, 187-195. https://doi.org/10.1093/cz/zoz039.

McEvoy, J., While, G. M., Sinn, D. L., Carver, S., & Wapstra, E. (2015). Behavioural syndromes and structural and temporal consistency of behavioural traits in a social lizard. *Journal of Zoology*, 296, 58-66. https://doi.org/10.1111/jzo.12217.

Martin, T. E., & Briskie, J. V. (2009). Predation on Dependent Offspring: A Review of the Consequences for Mean Expression and Phenotypic Plasticity in Avian Life History Traits. *Annals of the New York Academy of Sciences*, *1168*, 201-217. https://doi.org/10.1111/j.1749-6632.2009.04577.x.

Mathot, K. J., Dingemanse, N. J., & Nakagawa, S. (2019). The covariance between metabolic rate and behaviour varies across behaviours and thermal types: Meta-analytic insights. *Biological Reviews*, *94*, 1056-1074. https://doi.org/10.1111/brv.12491.

Montgomerie, R. D., & Weatherhead, P. J. (1988). Risks and rewards of nest defence by parent birds. *The Quarterly Review of Biology*, *63*, 167-187. https://doi.org/10.1086/415838.

Morinay, J., Daniel, G., Gustafsson, L., & Doligez, B. (2019). No evidence for behavioural syndrome and genetic basis for three personality traits in a wild bird population. *Animal Behaviour*, *153*, 69-82. https://doi.org/10.1016/j.anbehav.2019.05.001

Myers, R. E., & Hyman, J. (2016). Differences in measures of boldness even when underlying behavioral syndromes are present in two populations of the song sparrow (*Melospiza melodia*). *Journal of Ethology*, *34*, 197-206. https://doi.org/10.1007/s10164-016-0465-9.

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews*, *85*, 935-956. https://doi.org/10.1111/j.1469-185X.2010.00141.x.

Oro, D., Pradel, R., & Lebreton, J.-D. (1999). Food availability and nest predation influence life history traits in Audouin's gull, *Larus audouinii*. *Oecologia*, *118*, 438-445. https://doi.org/10.1007/s004420050746.

Øverli, Ø., Korzan, W. J., Höglund, E., Winberg, S., Bollig, H., Watt, M., Forster, G. L., Barton, B. A., Øverli, E., Renner, K. J., & Summers, C. H. (2004). Stress coping style predicts aggression and social dominance in rainbow trout. *Hormones and Behavior*, *45*, 235-241. https://doi.org/10.1016/j.yhbeh.2003.12.002.

Øverli, Ø., Sørensen, C., Pulman, K.G., Pottinger, T.G., Korzan, W., Summers, C.H. & Nilsson, G.E. (2007). Evolutionary background for stress-coping styles: relationships between physiological, behavioral, and cognitive traits in non-mammalian vertebrates. *Neuroscience & Biobehavioral Reviews*, *31*, 396-412. https://doi.org/10.1016/j.neubiorev.2006.10.006.

Pärt, T., & Gustafsson, L. (1989). Breeding dispersal in the collared flycatcher (*Ficedula albicollis*)-possible causes and reproductive consequences. *Journal of Animal Ecology*, *58*, 305-320. https://doi.org/10.2307/5002.

Patrick, S. C., & Weimerskirch, H. (2014). Personality, Foraging and Fitness Consequences in a Long Lived Seabird. *PLoS ONE*, *9*, e87269. https://doi.org/10.1371/journal.pone.0087269.

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

Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge University Press.

Rabdeau, J., Badenhausser, I., Gaffard, A., Mangelinck, C., Moreau, J., Bretagnolle, V., & Monceau, K. (2021). Assortative pairing for boldness and consequences for reproductive success in Montagu's harrier. *Biological Journal of the Linnean Society*, *132*, 759-773. https://doi.org/10.1093/biolinnean/blaa233.

R Core team. (2022). *Package 'parallel'*.

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

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 4051-4063. https://doi.org/10.1098/rstb.2010.0208.

Reaney, L. T., & Backwell P. R. Y. (2007). Risk-taking behaviour predicts aggression and mating success in a fiddler crab. *Behavioural Ecology*, *18*, 521-525. https://doi.org/10.1093/beheco/arm014.

Récapet, C., Daniel, G., Taroni, J., Bize, P., & Doligez, B. (2016). Food supplementation mitigates dispersal-dependent differences in nest defence in a passerine bird. *Biology Letters*, *12*, 20160097. https://doi.org/10.1098/rsbl.2016.0097.

Redondo, T. (1989). Avian nest defence: theoretical models and evidence. *Behaviour*, *111*, 161-195. https://doi.org/10.1163/156853989X00646.

Richardson, K. M., Parlato, E. H., Walker, L. K., Parker, K. A., Ewen, J. G., & Armstrong, D. P. (2019). Links between personality, early natal nutrition and survival of a threatened bird. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*, 20190373. https://doi.org/10.1098/rstb.2019.0373.

Ricklefs, R. E. (1970). Stage of taxon cycle and distribution of birds on Jamaica, greater Antilles. *Evolution. 24*, 475–477.

Rytkonen S. (2002). Nest defence in great tits *Parus major*: support for parental investment theory. *Behavioral Ecology and Sociobiology. 52*, 379–384. https://doi.org/10.1007/s00265-002-0530-y.

Shew, J. J., van der Merwe, J., Schauber, E. M., Tallitsch, B. K., & Nielsen, C. K. (2016). A classic question revisited in red-winged blackbirds: Disentangling confounding hypotheses surrounding parental investment theory and nest defense intensity. *Behavioral Ecology and Sociobiology*, *70*, 1843-1856. https://doi.org/10.1007/s00265-016-2190-3.

Short, K. H., & Petren, K. (2008). Boldness underlies foraging success of invasive *Lepidodactylus lugubris* geckos in the human landscape. *Animal Behaviour*, *76*, 429-437. https://doi.org/10.1016/j.anbehav.2008.04.008.

Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral Syndromes: An Integrative Overview. *The Quarterly Review of Biology*, *79*, 241-277. https://doi.org/10.1086/422893.

Sih, A., & Bell, A. M. (2008). Insights for behavioural ecology from behavioral syndromes. *Advances in the Study of Behavior 38*, 227-281. https://doi.org/10.1016/S0065-3454(08)00005-3.

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

Snijders, T. A. B., & Bosker, R. J. (1999). *Multilevel analysis: An introduction to basic and advanced multilevel modelling*. Sage.

Starling, M. J., Branson, N., Thomson, P. C., & McGreevy, P. D. (2013). Age, sex and reproductive status affect boldness in dogs. *The Veterinary Journal*, *197*, 868-872. https://doi.org/10.1016/j.tvjl.2013.05.019.

Strauss, R. E. (1990). Predation and life-history variation in *Poecilia reliculata* (Cyprinodontiformes : Poeciliidae). *Environmental Biology of Fishes*, *27*, 121-130. https://doi.org/10.1007/BF00001941.

Svensson, L. (1992). Identification Guide to European Passerines (4th ed.). Stockholm: Svensson.

Tabachnick, B. G. & Fidell, L. S. (1996). Using multivariate statistics. New York, NY: Harper Collins.

Tamin, T., & Doligez, B. (2022). Assortative mating for between-patch dispersal status in a wild bird population: Exploring the role of direct and indirect underlying mechanisms. *Journal of Evolutionary Biology*, *35*, 561-574. https://doi.org/10.1111/jeb.13925.

Toms, C. N., Echevarria, D. J., & Jouandot, D. J. (2010). A Methodological Review of Personality-Related Studies in Fish: Focus on the Shy-Bold Axis of Behavior. *International Journal of Comparative Psychology*, *23*, 1-25. https://escholarship.org/uc/item/949413qt.

Traisnel, G., & Pichegru, L. (2018). Does it always pay to defend one's nest? A case study in African penguin. *Ethology*, *124*, 74-83. https://doi.org/10.1111/eth.12704.

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual Selection and the Descent of Man*, *1871–1971* (pp. 378).

Ward-Fear, G., Brown, G. P., Pearson, D. J., West, A., Rollins, L. A., & Shine, R. (2018). The ecological and life history correlates of boldness in free-ranging lizards. *Ecosphere*, *9*, e02125. https://doi.org/10.1002/ecs2.2125.

Way, G. P., Kiesel, A. L., Ruhl, N., Snekser, J. L., & McRobert, S. P. (2015). Sex differences in a shoaling-boldness behavioral syndrome, but no link with aggression. *Behavioural Processes*, *113*, 7-12. https://doi.org/10.1016/j.beproc.2014.12.014.

Wiggins, D. A., Pärt, T., & Gustafsson, L. (1994). Seasonal decline in collared flycatcher Ficedula albicollis reproductive success: an experimental approach. *Oikos, 70*, 359-364. https://doi.org/10.2307/3545773.

Wiklund, C. G. (1990). Offspring protection by merlin *Falco columbarius* females; the importance of brood size and expected offspring survival for defense of young. *Behavioral Ecology and Sociobiology*, *26*, 217-223. https://doi.org/10.1007/BF00172089.

Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in Ecology and Evolution*, *27*, 452-461. http://doi.org/10.1016/j.tree.2012.05.001

Yoshida, M., Nagamine, M., & Uematsu, K. (2005). Comparison of behavioral responses to a novel environment between three teleosts, bluegill *Lepomis macrochirus*, crucian carp *Carassius langsdorfii*, and goldfish *Carassius auratus*. *Fisheries Science*, *71*, 314-319. https://doi.org/10.1111/j.1444-2906.2005.00966.x.

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

	Within-year				Between-year			
	With fixed effects		Without fixed effects		With fixed effects		Without fixed effects	
	PM	95% CI	PM	95% CI	PM	95% CI	PM	95% CI
Intercept	-2.71	[-9.85; 4.09]	2.09	[1.79; 2.38]	-0.63	[-7.05; 5.59]	2.28	[2.16; 2.38]
Fixed effects								
Sex (male)	**0.28**	**[0.15; 0.41]**			**0.28**	**[0.15; 0.40]**		
Age (yearling)	-0.03	[-0.16; 0.10]			-0.04	[-0.18; 0.09]		
Test order	**0.17**	**[0.07; 0.27]**						
Test date	0.09	[-0.19; 0.27]			0.07	[-0.09; 0.24]		
Test date^2	-0.00	[-0.00; 0.00]			-0.00	[-0.00; 0.00]		
Presence of the partner (present)	**0.93**	**[0.68; 1.18]**						
Random effects								
$V_{individual}$	0.73	[0.61; 0.87]	0.79	[0.66; 0.93]	0.57	[0.39; 0.77]	0.60	[0.41; 0.80]
$V_{observer}$	0.30	[0.15; 0.49]	0.29	[0.14; 0.47]				
$V_{year\text{-}patch}$	0.05	[0.01; 0.11]	0.06	[0.01; 0.12]	0.13	[0.06; 0.21]	0.14	[0.07; 0.22]
V_{dummy}	0.13	[0.02; 0.32]	0.13	[0.02; 0.30]		[		
V_{ε}	0.68	[0.59; 0.77]	0.70	[0.61; 0.80]	0.59	[0.42; 0.77]	0.59	[0.43; 0.76]
Number of observations	2101		2101		1384		1384	
Effective sample size	>3440		>2248		>2800		>2700	

Estimates for random effects are shown with and without fixed effects, and for the within- and between-year (i.e. all test values vs. one average value per individual per year) models. Posterior modes (PM) and 95% credible intervals (CI) are given. For categorical fixed effects, estimates refer to the category indicated within parentheses. $V_{individual}$ (*N* = 1228 with and without fixed effects) $V_{observer}$ (*N* = 27), $V_{year\text{-}patch}$ (*N* = 75), V_{dummy} (*N* = 10) and V_{ε} for within-year models indicate the variance associated to the individual identity, observer, the combination of year and patch, dummy and the residual variance, respectively, with $V_{\text{individual}}$ ($N = 1204$ with and without fixed effects), $V_{\text{year-patch}}$ ($N = 75$) and V_{ε} for between-year models the variance associated to individual identity, the combination of year and patch and the residual variance respectively. Estimates whose 95% CI do not encompass zero are shown in bold; fixed and random effects not estimable in between-year models are left empty.

Table 2. Variance explained by the two principal components in the PCA of the three behavioural traits

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

Variance explained and component loadings (*N* = 688) for the three behavioural traits under study. Loadings above the threshold of 0.32 are shown in bold.

Table 3. Phenotypic correlation between boldness, aggressiveness and neophobia scores and its components, i.e. among- and within-individual and environmental correlations

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

Number of observations (*N*), posterior modes and 95% credible intervals (CI) are given. Estimates whose 95% CI do not encompass zero are shown in bold.

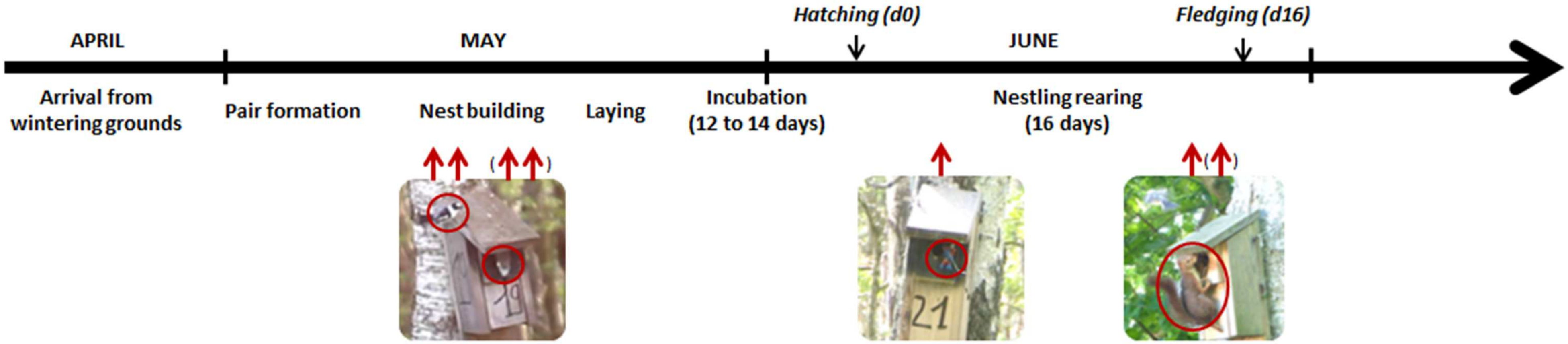
Figures

Figure 1. Graphical representation summarising the timing along the breeding season and main features of the three experimental tests: context, trait measured, stimulus used (with numbers of sets used to avoid pseudoreplication), timing of the test (breeding phase and time of the day), test duration, mode of recording and score computed. The red arrows indicate how many tests could be performed in each case (up to 4 for the aggressiveness test, 1 for the neophobia test and up to 2 for the boldness test) and their timing (maximum one test per day in the sequence). The red circles show an illustration of the stimulus used in each case (here, a pair of dummy flycatchers for the aggressiveness test, one at the nest entrance and one on the roof (for interspecific competition, only one great tit dummy was used, placed at the nestbox entrance), accompanied by the broadcast of the song of the species concerned; a blue and red 7-cm high plastic figurine for the neophobia test; and a red squirrel for the boldness test). The timing of breeding phases is illustrated for an average year here but could vary depending on years.

Figure 2. Posterior mode and 95% CI of the effect of the boldness-aggressiveness syndrome measured by (a) the first principal component of the PCA between the three behavioural scores considered here, boldness, aggressiveness and neophobia (PC1) and its square value (PC1²) or (b) the interaction between the aggressiveness and boldness scores (denoted aggr:bold) on the number of fledged young and their recruitment probability. Estimates were obtained over the 100 randomisations used to select one parent randomly when both were scored (see text).

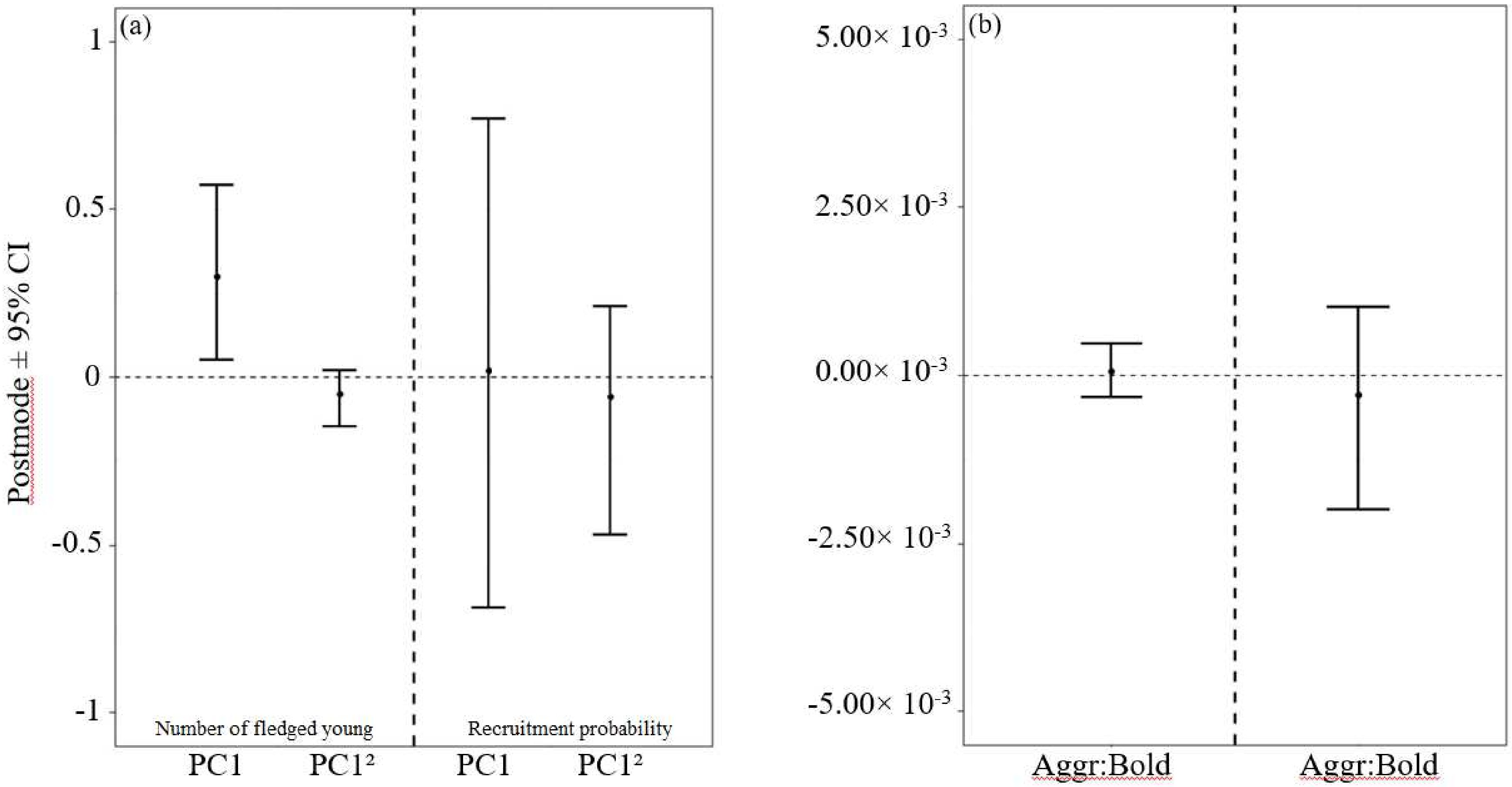
Figure 3. Number of fledged young depending on the first principal component of a PCA between the three behavioural scores considered here (boldness, aggressiveness, neophobia) as a measure of the boldness-aggressiveness syndrome. We present for illustration here one of the 100 randomisations used to select one parent when both were scored (see text). Data points as well as posterior mode (line) ± 95% credible interval (grey area) of the estimate coefficient are shown; estimates were obtained from the model including the first principal component, its squared value, sex, age, laying date and laying date^2 as fixed effects, and individual identity and the combination between patch and year as random factors.

Figure 1



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

Figure 2


(a)
Postmode ± 95% CI
1
0.5
0
-0.5
-1
Number of fledged young
Recruitment probability
PC1
PC1²
PC1
PC1²
(b)
5.00× 10-3
2.50× 10-3
0.00× 10-3
-2.50× 10-3
-5.00× 10-3
Aggr:Bold
Aggr:Bold

1087 Figure 3