

# Assortative pairing for boldness and consequences for reproductive success in Montagu's harrier

JULIETTE RABDEAU<sup>1,\*</sup>, ISABELLE BADENHAUSSER<sup>2</sup>, AGATHE GAFFARD<sup>1</sup>, CAMILLE MANGELINCK<sup>1</sup>, JÉRÔME MOREAU<sup>1,3</sup>, VINCENT BRETAGNOLLE<sup>1,4</sup> and KARINE MONCEAU<sup>1</sup>

<sup>1</sup>UMR 7372, Centre d'Etudes Biologiques de Chizé, La Rochelle Université & CNRS, 79360 Villiers en Bois, France

<sup>2</sup>INRAE, Unité de Recherche Pluridisciplinaire Prairies Plantes Fourragères, F-86600 Lusignan, France

<sup>3</sup>UMR CNRS 6282 Biogéosciences, Équipe Écologie Évolutive, Université de Bourgogne-Franche-Comté, 21000 Dijon, France

<sup>4</sup>LTSER 'Zone Atelier Plaine & Val de Sèvre', CNRS, 79360 Villiers-en-Bois, France

Received 27 November 2020; revised 22 December 2020; accepted for publication 24 December 2020

Behavioural combination within pairs depending on personality and plasticity might influence reproductive success. However, studies testing this hypothesis are rare, especially in the case of monogamous species with bi-parental care in which the sexes exhibit different behavioural roles. In this study, we investigated the pairing patterns for both boldness and boldness plasticity in Montagu's harriers (*Circus pygargus*), a species with sex-specific care, and the consequences for their reproductive success. We measured individual boldness and plasticity for both sexes, and we assessed the pairing pattern in the Montagu's harrier population for these two traits. We calculated four indices to characterize the behavioural association within pairs: pair boldness, boldness similarity within pairs, pair plasticity and plasticity similarity within pairs. The relationship between the behaviour of the parents and the reproductive success was then tested through these four indices. We found a pattern of assortative pairing based on both boldness and plasticity in the Montagu's harrier population. Within-pair similarity of plasticity had a significant effect on the reproductive success, which was higher for less similar pairs than for more similar pairs. Our results question the origin of this pairing pattern and suggest that ecological constraint and not sexual selection could be the major driver.

**ADDITIONAL KEYWORDS:** behavioural reaction norms – behavioural similarity – flight initiation distance – personality – plasticity – sexual selection.

## INTRODUCTION

Random mating rarely occurs in the animal kingdom, and assortative pairing (i.e. the observed pattern of association between males and females for a character within a population) is prevalent across many taxa for genetic or phenotypic traits (reviewed by Jiang *et al.*, 2013). Assortative pairing can be either positive, if males and females are paired according to similar trait values, or negative, if they are paired for opposite values of the trait (also called disassortative pairing). Many studies have investigated pairing patterns with regard to genetic

traits (major histocompatibility complex; Bonneaud *et al.*, 2006; Ortego *et al.*, 2009), age (Black & Owen, 1995; Ludwig & Becker, 2008), body size (da Silva Castiglioni & Bond-Buckup, 2008; Pack *et al.*, 2012), coloration (MacDougall & Montgomerie, 2003; Pérez i de Lanuza *et al.*, 2013; Fargevieille *et al.*, 2017) and behavioural traits (Gabriel & Black, 2012). Assortative mating can result from sexual selection (e.g. mate choice; Schuett *et al.*, 2010) and should thus provide fitness benefits to both partners (Masumoto, 1999; Daunt *et al.*, 2003; Ariyomo & Watt, 2012) through an increase in reproductive success (Faivre *et al.*, 2001; Masello & Quillfeldt, 2003; Bitton *et al.*, 2008). Alternatively, assortative mating can result from a non-random spatial or temporal distribution

\*Corresponding author. E-mail: [juliette.rabdeau@gmail.com](mailto:juliette.rabdeau@gmail.com)

of phenotypes/genotypes within the environment (Ferrer & Penteriani, 2003; Flockhart & Wiebe, 2007; Servedio & Boughman, 2017; Wang *et al.*, 2019). For example, in Spanish imperial eagles (*Aquila adalberti* Brehm, 1861), individuals differ in their spatial distribution in the landscape depending on their age, thus inducing a positive age-assortative pairing in the population (Ferrer & Penteriani, 2003). In this case, fitness benefits are not necessarily expected (Ferrer & Penteriani, 2003; Flockhart & Wiebe, 2007).

Among the behavioural traits of interest for assortative mating, personality traits (i.e. constant behavioural differences among individuals; Réale *et al.*, 2007; Dingemanse *et al.*, 2010), such as activity (Montiglio *et al.*, 2016), aggressiveness towards conspecifics (Harris & Siefferman, 2014), boldness (i.e. risk-taking behaviour; Traisnel & Pichegru, 2017; Clermont *et al.*, 2019) or exploration (Both *et al.*, 2005), have been investigated in particular (reviewed by Schuett *et al.*, 2010). The combination of personalities within pairs can influence their reproductive success through parental investment, especially in species with bi-parental care (Kontiaainen *et al.*, 2009; Schuett *et al.*, 2010, 2011). More similar partners would be more effective in cooperating and coordinating their activities, such as food provisioning and/or nest defence (Spoon *et al.*, 2006; Schuett *et al.*, 2010, 2011; Gabriel & Black, 2012; Harris & Siefferman, 2014; Burtka & Grindstaff, 2015). For example, in zebra finches (*Taeniopygia guttata* Vieillot, 1817), partners with similar aggressiveness have fledglings in better body condition because of reduced sexual conflicts between them over food provisioning (Schuett *et al.*, 2011). In a similar manner, a pairing pattern might also occur for behavioural plasticity (Royle *et al.*, 2010; Schuett *et al.*, 2011). Behavioural plasticity represents the ability of individuals to be flexible in their behaviour depending on environmental conditions and is often correlated with personality (Nussey *et al.*, 2007; Dingemanse *et al.*, 2010; Betini & Norris, 2012). For example, shy individuals might show greater behavioural plasticity than bold individuals because of their higher sensitivity to environmental variations (Koolhaas *et al.*, 1999, 2010; Zidar *et al.*, 2017).

Few studies have investigated the fitness consequences of pairing pattern while accounting for both personality and behavioural plasticity (but see Royle *et al.*, 2010; Schuett *et al.*, 2010). Only one study has examined the effects of personality and behavioural plasticity within pairs on reproductive success (Schuett *et al.*, 2011). Captive zebra finch partners with similar exploration plasticity (both partners with either low plasticity or high plasticity) have nestlings in better body condition than dissimilar partners, possibly owing to higher coordination in parental care. This

example, however, concerns a species with bi-parental care but similar roles between sexes. Studies focusing on species that exhibit sex-specific parental care roles are rare in this context. For these species, the behavioural similarity within pairs could be of interest because sexual conflicts are more likely to occur (see the review by Royle *et al.*, 2010). Indeed, if one partner reduces its parental investment, the other one might not compensate (Royle *et al.*, 2010). A similarity in personality and plasticity between partners might thus provide greater behavioural compatibility, a reduction in sexual conflicts, higher parental investment and, consequently, higher reproductive success (Spoon *et al.*, 2006; Royle *et al.*, 2010; Schuett *et al.*, 2010; Ihle *et al.*, 2015).

The aim of the present study was to test whether higher similarity within pairs for both personality and plasticity might increase fitness in a species with bi-parental care but different roles between sexes. Our study model is Montagu's harrier (*Circus pygargus* Linnaeus, 1758), a raptor species with separate sex-specific care. The female is responsible for incubation and care at the nest, while the male hunts and brings prey to feed his female and chicks (see the review by Arroyo *et al.*, 2004). Nest defence is performed by both sexes but occurs at different scales. The female stays near to the nest most of the time, whereas the male can be away for long periods during hunting sessions (Mougeot *et al.*, 2001, 2006). A long-term study conducted on this species showed that shy females experience more nest failures and lower productivity than bold females (Arroyo *et al.*, 2017). However, the effect of male boldness has not been tested, either alone or combined with female behaviour.

In the present study we explore, for the first time, the pairing pattern linked to both the boldness trait (i.e. risk-taking behaviour towards humans, hereafter termed boldness) and boldness plasticity (i.e. within-individual variability in risk-taking behaviour towards humans, hereafter termed plasticity) and its relationship to reproductive success in natural conditions. First, we assessed boldness and plasticity for both sexes during three consecutive breeding seasons in intensive farmland in western France. Second, we investigated the pairing pattern for boldness and plasticity. Finally, we examined the relationship between the behavioural association within pairs and their reproductive success, using four indices characterizing pair boldness and plasticity and the similarity of the partners within pairs for their boldness and plasticity. We predicted that partners should be paired assortatively for boldness and plasticity because behavioural similarity should decrease sexual conflicts, improve parental investment and thus, enhance fitness through reproductive success.

## MATERIAL AND METHODS

### ETHICS STATEMENT

Nest visits were allowed by a permit from the CRBPO (Centre de Recherches sur la Biologie des Populations d'Oiseaux, Museum National d'Histoire Naturelle, licence #1308).

### STUDY SITE AND MODEL SPECIES

The study was focused on a population of Montagu's harriers extensively monitored since 1995 within the Long-Term Socio-Ecological Research (LTSER) Zone Atelier Plaine & Val de Sèvre (hereafter termed ZAPVS; western France, 46°110'N, 0°280'W), covering ~435 km<sup>2</sup> of intensive farmlands (Bretagnolle *et al.*, 2018). Montagu's harrier is a threatened, protected species that nests on the ground, mainly in cereal crops, making chicks and adults vulnerable to agricultural work, especially during the cereal harvesting period (Arroyo *et al.*, 2002; Millon *et al.*, 2002). The number of pairs nesting in the ZAPVS varies according to the abundance of small mammals, and especially its main prey, the common vole (*Microtus arvalis* Pallas, 1778) (Millon *et al.*, 2008; Millon & Bretagnolle, 2008). In years of high abundance in small mammals, ≤ 100 pairs nest in ZAPVS (Arroyo *et al.*, 2003), but over the last 3 years (2017–2019) only ~40 pairs did so. In France, the population of Montagu's harriers is decreasing, probably owing to the intensification of agricultural practices in recent decades, thus making them of high conservational priority (Butet & Leroux, 2001; Santangeli *et al.*, 2015). Adult females lay up to six eggs (Millon *et al.*, 2008). The incubation period usually begins in early May for the earliest pairs and lasts 29 days on average, and the rearing period lasts for 30–35 days (García & Arroyo, 2001; Arroyo *et al.*, 2004).

In our study population, a few individuals are marked with wing tags or Global Positioning System (GPS) devices (marked individuals/total number of individuals: 2017, 24 of 43 males and 12 of 43 females; 2018, 19 of 40 males and 17 of 40 females; and 2019, five of 40 males and eight of 40 females). Trapping adult Montagu's harriers is challenging, especially for the males. Females can be captured more easily at the nest, but the stress for both the female and the chicks can be high. The most effective strategy would be to tag all juveniles before fledging, but philopatry is low (< 5% of the tagged juveniles return to within 10 km of their natal nest, Limiñana *et al.* 2012a; see also Chadœuf *et al.*, 2018). Given that nest site fidelity might also depend on reproductive success (which might be affected by trapping), it is almost impossible to tag all individuals in this population every year

without impacting the reproduction of this declining species.

### NEST MONITORING AND REPRODUCTIVE SUCCESS

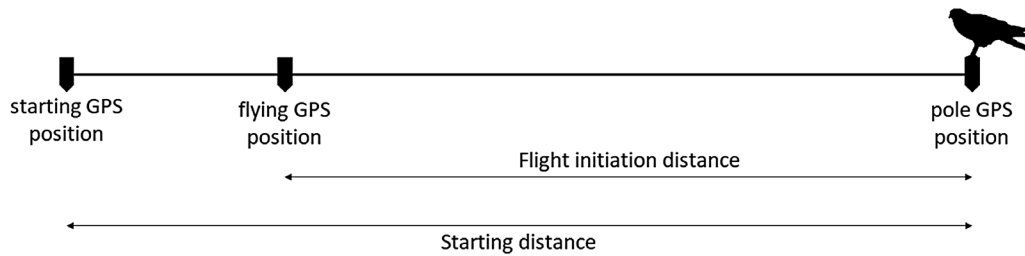
In 2017, 2018 and 2019, Montagu's harrier nests were localized in the ZAPVS (43, 40 and 40 nests found, respectively). We visited them twice during incubation and five times during the chick-rearing period (from hatching to fledging; lag time between visits:  $7 \pm 2$  days), depending on brood size and differences in hatching dates. We measured egg length and width using callipers (accuracy:  $\pm 0.1$  mm) and egg mass using a Pesola electronic scale (accuracy:  $\pm 0.1$  g) during incubation, following Arroyo *et al.* (2017), because changes in egg density allow prediction of the hatching date. The final clutch size was also noted. After hatching, the first visit occurred when the first nestlings were  $7 \pm 2$  days old; the two first visits allowed counting the number of hatched eggs to estimate hatching failure. At the end of the breeding period, we conducted the last visit to check fledging success. We performed behavioural measurements on female and male adults from nest discovery until fledging (i.e. from the end of April to July).

### ADULT BEHAVIOURAL MEASURES

The flight initiation distance (FID) is the distance at which the individual begins to fly when a predator (such as a human) approaches (Frid & Dill, 2002). The FID is considered an anti-predator behaviour, and it is often used to estimate the individual boldness as risk-taking behaviour (Blumstein, 2006; Carrete & Tella, 2010; Selmann *et al.*, 2012; Møller *et al.*, 2013). Therefore, we measured the FID for Montagu's harrier males and females to estimate their boldness. Note that male and female FIDs within a pair were measured by different experimenters to avoid any bias attributable to this factor (Class *et al.*, 2017; Wang *et al.*, 2019).

#### *Measurement of male boldness*

Once a nest had been located in a field, we positioned a pole close to the nest in the border of the field along a path or a road, allowing the male to perch, and its GPS location was noted using a GARMIN GPS (eTrex@ 20x) ('pole GPS position'; Figure 1). We systematically checked male identification with behavioural observations of the male and female (e.g. food provisioning) in addition to wing tags, a GPS device or morphological features. During breeding, we checked the nest surroundings for males standing on the pole between 06.00 and 12.00 h (with favourable weather conditions, i.e. no rain and with wind speed < 30 km h<sup>-1</sup>). When a male was found, the experimenter



**Figure 1.** Experimental design to measure male flight initiation distance. For each approach, the distance between the Global Positioning System (GPS) position of the start and the GPS position of the pole (i.e. position of the focal male) allowed calculation of the starting distance. The flight initiation distance represented the distance between the GPS position of the experimenter at the time of flight and the GPS position of the pole.

approached it from a starting distance of  $\sim 200$  m, depending on landscape configuration ('starting GPS position'; Figure 1). The experimenter walked straight towards the focal individual at a constant speed ( $\sim 1.0$  m s<sup>-1</sup>). When the focal bird initiated flight, the experimenter stopped and recorded his GPS coordinates ('flying GPS position') to calculate the male FID (Figure 1). For all approaches, the experimenter was visible from the start to the end of the approach, and thus all males were able to detect him visually throughout the approach. We performed at least two approaches per individual during the breeding season, with an interval of  $7.87 \pm 5.45$  days (mean  $\pm$  SD,  $N = 107$  observations). The starting distance was not the same between different approaches for a given male, in order to study the behavioural response to this fluctuating factor (i.e. plasticity). It was also different between males depending on the landscape configuration. The FID was measured for 13 males in 2017 (36 observations;  $2.77 \pm 0.83$  approaches per individual), 13 males in 2018 (33 observations;  $2.54 \pm 0.52$  approaches per individual) and 13 males in 2019 (38 observations;  $2.92 \pm 0.86$  approaches per individual), with no differences among males in the number of repeated approaches ( $\chi^2$  test:  $\chi^2 = 9.13$ , d.f. = 38,  $P = 1.0$ ). Obtaining repeated measures of male FID is challenging, because males spent their time hunting for prey, flying for long distances, and are thus in the vicinity of the nest for only a few moments during the day. We recorded different factors that can influence the FID, at each approach: the starting distance, the rank of approaches (i.e. the order of FID measurements per individual) and the nesting stage estimated according to the date of each approach relative to the first laid egg, which was set as day 1.

### Measurement of female boldness

Given that females rarely used the pole during incubation, FID measurements were made when approaching the nest and only with favourable weather conditions (i.e. no rain and with wind speed  $< 30$

km h<sup>-1</sup>). We measured female FID as the distance at which a female on the nest initiated a flight when an experimenter approached to visit the nest (for details, see Arroyo *et al.*, 2017). The experimenters (between one and three people, depending on the visit; see below in this section) walked straight to the nest at a constant speed ( $\sim 1.0$  m s<sup>-1</sup>) across the field crop. When the female flew out of the nest, the experimenter stopped and counted his steps to the nest to measure female FID. The number of experimenters was usually one person during incubation visits ( $1.12 \pm 0.40$ ,  $N = 113$  visits) and usually three people for visits during the rearing period ( $2.78 \pm 0.51$ ,  $N = 290$  visits). We measured female FID at least twice for 27 females in 2017 (79 observations,  $2.93 \pm 0.78$  approaches per individual), 16 in 2018 (42 observations,  $2.63 \pm 0.80$  approaches per individual) and 23 in 2019 (60 observations,  $2.63 \pm 0.80$  approaches per individual). At each nest visit, we noted different factors that can influence female FID: the rank of approaches and the nesting stage. Additionally, given that nests are hidden in crop vegetation, detection of the experimenter by the females relies mainly on noise cues. For this reason, the experimenter's starting distance did not affect female FID, whereas we expected FID to be influenced by the number of experimenters (i.e. the more numerous the experimenters, the more noise they make).

## STATISTICAL ANALYSES

### Repeatability of FID

The repeatability of Montagu's harrier FID over time was analysed for sexes and years separately. Repeatability is a condition that needs to be met in order to consider a behavioural trait as a personality trait. We checked the normality and the homoscedasticity of FID with Shapiro–Wilk and Levene's tests, respectively. We estimated the FID repeatability coefficients (hereafter  $R$ , ranging from zero, non-consistent, to one, highly consistent) using linear mixed-effects models (LMMs) using

*rptR* (Nakagawa & Schielzeth, 2010) and *lmerTest* packages (Kuznetsova *et al.*, 2014), including the identity of the individual as a random effect.

### Factors influencing FID

To explore the factors that impacted individual FID, we used LMMs and followed the within-subject centring (WSC) method proposed by van de Pol & Wright (2009). This method is advocated for the analysis of behavioural reaction norms and for *in natura* studies when individuals cannot be measured in the same conditions (see Dingemanse *et al.*, 2010). It enables discrimination between the behavioural variability linked to within-individual variation (i.e. behavioural plasticity across contexts) and the behavioural variability linked to between-individual variation (i.e. some behaviours occurred more often in specific environmental conditions). In the present study, for instance, all males could not be measured at the same starting distance owing to differences in the landscape configuration around each pole. Consequently, the WSC method allows identification of whether the behavioural response is explained by a between-individual or a within-individual effect of each explanatory variable (van de Pol & Wright, 2009). In our design, the nesting stage was correlated with the rank of approaches for both sexes (Spearman's rank correlation test, males,  $\rho = 0.27$ ; 95% confidence interval [CI] = [0.09; 0.44]; and females,  $\rho = 0.70$ ; 95% CI = [0.60; 0.77]). In addition, for females, the rank of approaches was also correlated with the number of experimenters ( $\rho = 0.62$ ; 95% CI = [0.52; 0.72]). To avoid collinearity issues, we retained only the rank of approaches and the starting distance as fixed effects in the LMM for males. Likewise, for females, we retained only the rank of approaches as a fixed effect in the LMM. The rank of approaches was preferred to the number of experimenters to examine also the potential effects of habituation/sensitization across repeated approaches (for an example of sensitization in Montagu's harrier chicks, see Rabdeau *et al.*, 2019). Explanatory variables (for males, starting distance and rank of approaches; and for females, rank of approaches) were centred and scaled. Then, for the starting distance, we calculated the between-individual variability (hereafter, between) using the mean value of the starting distance, for each male (van de Pol & Wright, 2009; Dingemanse *et al.*, 2010). For each observation of a male, we calculated the within-individual variability (hereafter, within) using the deviation from the mean value of starting distance previously computed (van de Pol & Wright, 2009; Dingemanse *et al.*, 2010). The between and within effects of starting distance were included in

the LMM for males. Individual identity was included as a random effect in LMMs. The random intercept allowed an estimation of the personality of each individual (see below in the next section). The rank of approaches was included as a fixed effect in LMMs, for both males and females. For each LMM (one per sex), the normality of residuals was compliant.

### Individual boldness and boldness plasticity based on FID

From the LMMs described above, we assessed differences among individuals in the slope for the relationship between FID and the significant explanatory variable (the starting distance for males or the rank of approaches for females; see Results) (van de Pol & Wright, 2009; Dingemanse *et al.*, 2010, 2012; Carter *et al.*, 2012). For each sex, we compared the LMM with both random intercepts on the identity of the individual and random slopes on the considered explanatory variable with the same LMM without a random slope, using a likelihood-ratio  $\chi^2$  test. This allows assessment of whether individuals differed from each other in their plasticity. Results from LMMs with random slopes and random intercepts are presented here. Finally, we extracted the intercept and slope for each individual from an LMM with random slopes and random intercepts for each sex. Consequently, for each individual, the intercept represented the boldness personality (hereafter termed boldness, with high values representing shy individuals and low values bold individuals) and the slope represented the boldness plasticity (hereafter termed plasticity).

Next, we used the absolute value of the slope (i.e. whether individuals are plastic or not, with high values representing plastic individuals and low values not-plastic individuals) for each individual. We chose to use the absolute values of slopes to describe boldness plasticity in males and females for two reasons. First, we were interested in whether individuals displayed plasticity (non-horizontal slope) or not (horizontal slope) and not in the way the plasticity is displayed (i.e. the sign of the slope: increasing or decreasing response along the gradient used for the measurement; Dingemanse *et al.*, 2010). Second, even if we were interested in the way the plasticity is expressed, our small sample size limits the use of the sign of the slope for analyses. Among females and males, only two out of 39 and eight out of 66 had negative slopes, respectively; thus, this low variability in the sign of the slope did not allow the testing of such differences for analyses at the pair level (see below in the next section). For each sex, we tested the link between boldness and plasticity using Spearman's rank correlation tests, because variable distribution did not meet the assumption of normality.

### Pairing patterns

Given that the study was conducted in natural conditions, it was difficult to measure both female and male FID successfully within all pairs. The pairing pattern could be analysed for 30 pairs (2017, 12 pairs; 2018, six pairs; and 2019, 12 pairs). Boldness and plasticity were tested separately using Spearman's rank correlation tests to establish how males and females were paired. For correlation tests, the statistical significance is highly dependent on the sample size; for example, as a result of a large sample size, a small correlation coefficient without any biological meaning might be significant (see Nakagawa & Cuthill, 2007). Therefore, we considered the effect size (i.e. correlation coefficient) and, following Cohen *et al.* (1988), a correlation coefficient ( $\rho$ ) of 0.1, 0.3 or 0.5 as a 'small', 'medium' or 'large' effect, respectively. We performed a power analysis using the *pwr* package (Champely *et al.*, 2018) to assess the power of our Spearman's rank correlation tests (for more details, see Supporting Information, Appendix S1; Table S1).

Also, we calculated four indices for each pair to characterize behavioural association within pair: pair boldness, boldness similarity within pairs, pair plasticity and plasticity similarity within pairs. To do so, we performed two principal components analyses (PCAs; one for boldness and one for plasticity) using a singular value decomposition of the centred and scaled data matrix (Crawley, 2012). The PCA allows avoidance of a cause-and-effect relationship between male and female behaviour and is equivalent to an orthogonal regression in this case. The PCA for boldness (*PCAbold*) was conducted with female and male boldness, and the PCA for plasticity (*PCAplast*) was conducted with female and male plasticity. The first axis of *PCAbold* accounted for 68.9% of the overall variance. It was positively correlated with female boldness ( $r = 0.83$ ) and male boldness ( $r = 0.83$ ), representing the pair boldness (with a gradient from bold pairs having low values to shy pairs having high values). The second axis of *PCAbold* accounted for 31.1% of the overall variance. It was negatively correlated with female boldness ( $r = -0.56$ ) and positively with male boldness ( $r = 0.56$ ). The absolute values of the second axis represented the boldness similarity within pairs (with a gradient from more similar pairs having low values to less similar pairs having high values). The first axis of *PCAplast* accounted for 55.8% of the overall variance. It was positively correlated with female plasticity ( $r = 0.75$ ) and male plasticity ( $r = 0.75$ ) and represented the pair plasticity (with a gradient from not-plastic pairs having low values to plastic pairs having high values). The second axis of *PCAplast* accounted for 44.2% of the overall variance. It was negatively correlated with female plasticity ( $r = -0.67$ )

and positively with male plasticity ( $r = 0.67$ ), and its absolute values represented the plasticity similarity within pairs (with a gradient from more similar pairs having low values to less similar pairs having high values).

### Effects of pairing patterns on reproductive success

We assessed the effects of the behavioural association within pairs on two reproductive parameters: the number of fledglings and the fledging success (number of fledglings/clutch size). We tested the effects of either pair boldness and boldness similarity or pair plasticity and plasticity similarity on the two reproductive parameters. For the number of fledglings, we used a generalized linear mixed-effects model with a negative binomial error (NBGLMM), using 'quasi-Poisson' parameterization (i.e. variance strictly proportional to the mean, from the *glmmADMB* package; Bolker *et al.*, 2012). For the fledging success, we used a generalized linear mixed-effects model with a binomial error distribution (BGLMM). For each reproductive parameter, we performed two models including as explanatory variables: (1) pair boldness and boldness similarity; and (2) pair plasticity and plasticity similarity.

Given that few individuals (males or females) had wing tags or a GPS device in our study population, we did not know, for each individual, the number of years for which it was measured. Among marked individuals, only three males and six females were measured in 2 years. Consequently, we included the year as a random effect in all models (LMMs, NBGLMMs and BGLMMs). For all models, we used model comparisons with likelihood ratio-based  $\chi^2$ -statistics to estimate the statistical significance of explanatory variables, using the *car* package (Fox & Weisberg, 2011; Fox *et al.*, 2012). All statistical analyses were performed with R software (3.5.1; R Core Team, 2018).

## RESULTS

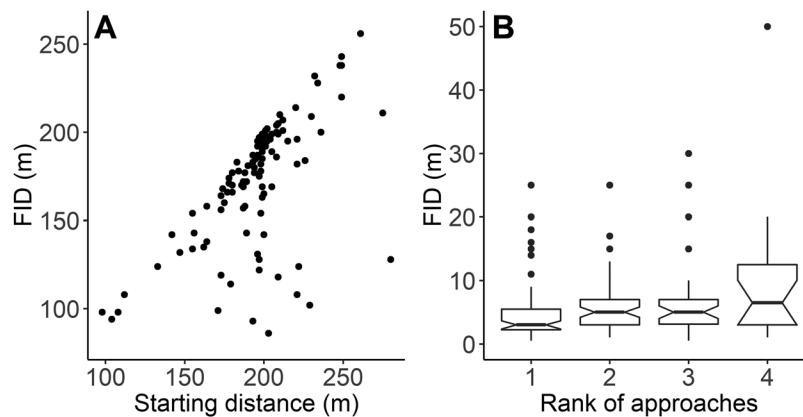
### FLIGHT INITIATION DISTANCE AND ITS REPEATABILITY

A summary of male and female FID, in addition to their repeatability, is given in Table 1. The FID repeatability was significant for both sexes whatever the year (Table 1). For males, the FID increased with the starting distance (i.e. the within effect; LMM,  $\chi^2 = 14.07$ , d.f. = 1,  $P < 0.001$ ; Fig. 2A). The significant between effect suggested variations among males in their FID and also attested that males were measured in different landscapes (and thus with different starting distances;  $\chi^2 = 39.22$ , d.f. = 1,  $P < 0.001$ ). The rank of approaches did not have

**Table 1.** Mean and 95% confidence interval of flight initiation distance (in metres) and repeatability of flight initiation distance for both sexes of adult Montagu's harriers

Year	Sample size	Flight initiation distance (m, mean [95% CI])	Repeatability [95% CI]
Males			
2017	13	169.39 (154.26; 184.52)	<b>0.41 (0.01; 0.70)</b>
2018	13	170.33 (157.52; 183.14)	<b>0.65 (0.26; 0.85)</b>
2019	13	176.71 (166.80; 186.63)	<b>0.50 (0.09; 0.74)</b>
Females			
2017	27	5.84 (4.80; 6.89)	<b>0.37 (0.08; 0.60)</b>
2018	16	6.36 (4.52; 8.20)	<b>0.61 (0.25; 0.81)</b>
2019	23	6.98 (4.86; 9.11)	<b>0.34 (0.02; 0.60)</b>

Values of repeatability significantly greater than zero are shown in bold. Abbreviation: CI, confidence interval.



**Figure 2.** A, effect of the starting distance (in metres) on the flight initiation distance (FID; in metres) in males. Each point represents one approach. B, effect of the rank of approaches on the FID (in metres) in females. The boxplot represents the median (thick lines within boxes), 25% and 75% quartiles (boxes), 1.5 times the interquartile range (whiskers) and extreme values (points).

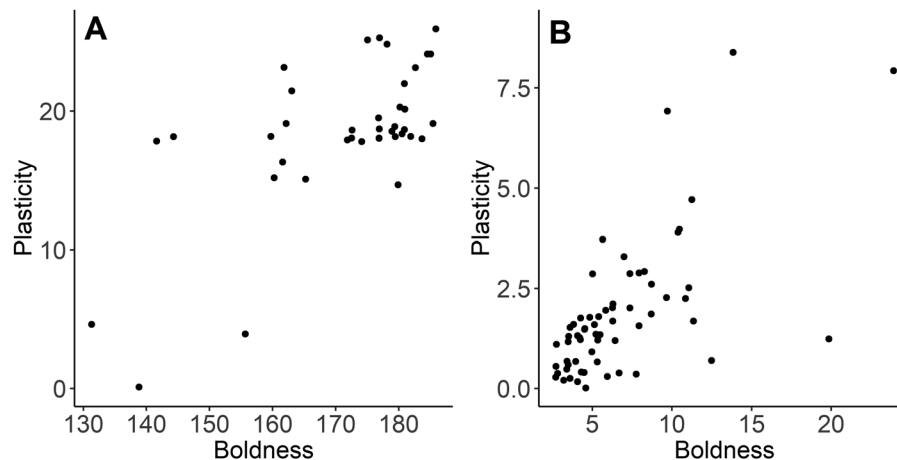
any effect on male FID ( $\chi^2 = 0.61$ , d.f. = 1,  $P = 0.43$ ). Conversely, in females, FID increased with the rank of approaches (LMM,  $\chi^2 = 9.26$ , d.f. = 1,  $P = 0.002$ ; Fig. 2B).

#### BOLDNESS AND PLASTICITY OF INDIVIDUALS AND PAIRING PATTERNS

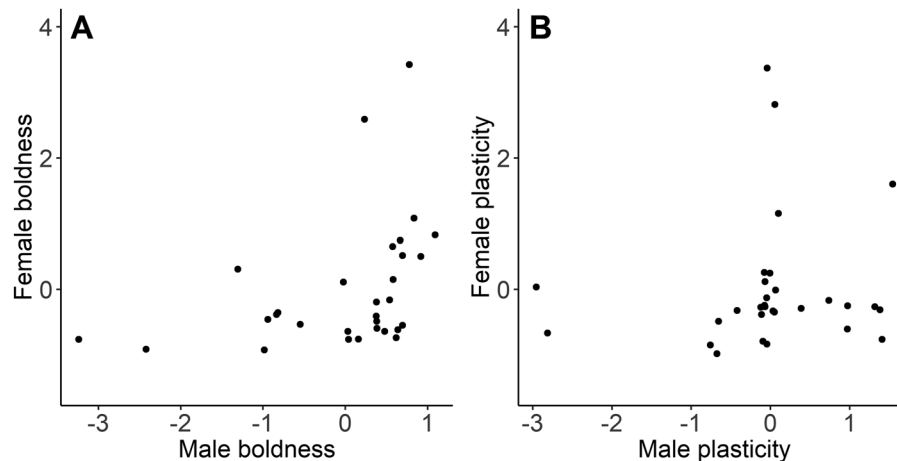
Males did not differ from each other in their plasticity (i.e. slope of the regression, likelihood ratio test,  $\chi^2 = 2.28$ , d.f. = 1,  $P = 0.13$ ). Male boldness was positively correlated with their plasticity (Spearman's rank correlation test,  $\rho = 0.55$ , 95% CI = [0.25; 0.76]; Fig. 3A). Conversely, females differed from each other in their plasticity (likelihood ratio test,  $\chi^2 = 14.75$ , d.f. = 1,  $P < 0.001$ ), but as in males, their boldness was positively correlated with their plasticity ( $\rho = 0.65$ , 95% CI = [0.47; 0.79]; Fig. 3B).

Male and female boldness were positively correlated when pooling years ( $\rho = 0.54$ , 95% CI = [0.17; 0.77]; Fig. 4A). When considering each year separately, the magnitude of correlations was medium (2019,  $\rho = 0.36$ , 95% CI = [-0.39; 0.86]) to large (2017,  $\rho = 0.73$ , 95% CI = [0.10; 0.96]; and 2018,  $\rho = 0.54$ , 95% CI = [-1.0; 0.80]). The confidence intervals for each year overlapped; thus, the correlations are considered similar. The sample size (2017, 12 pairs; 2018, six pairs; and 2019, 12 pairs) could explain the lack of statistical power. Power analyses showed that the correlations for 2018 and 2019 would be significant with sample sizes approximately five times larger than they were (for more details, see Supporting Information, Appendix S1).

Although males did not differ from each other in their plasticity, we chose to assess the pairing pattern for plasticity in the same way as for boldness.



**Figure 3.** Observed values of boldness [i.e. intercept from linear mixed-effects model (LMM) for each sex] and plasticity (i.e. slope from LMM for each sex) for each individual male (A) and female (B). For each individual, boldness and plasticity were estimated as the intercept and slope, respectively, from the LMM for each sex separately.



**Figure 4.** A, observed values of boldness [i.e. individual intercept from the linear mixed-effects model (LMM) for each sex]. B, observed values of plasticity (i.e. individual slope from LMM for each sex), showing positive assortative pairing patterns. Each point indicates a pair.

Male and female plasticity showed a medium positive correlation when considering all years pooled [ $\rho = 0.29$ , 95% CI = (-0.08; 0.62); Fig. 4B]. A lack of statistical power could also explain why the confidence interval slightly overlapped zero ( $N = 30$  pairs). Power analyses showed that with a sample size approximately three times larger, the correlation would be significant (for more details, see Supporting Information, Appendix S1). When considering each year separately, correlations were medium [2018,  $\rho = 0.26$ , 95% CI = (-0.94; 1.0); and 2019,  $\rho = 0.29$ , 95% CI = (-0.34; 0.72)] to large [2017,  $\rho = 0.45$ , 95% CI = (-0.35; 0.85)]. The confidence

intervals from each year overlapped; thus, the correlations are considered similar.

#### EFFECTS OF BOLDNESS AND PLASTICITY PAIRING PATTERNS ON REPRODUCTIVE SUCCESS

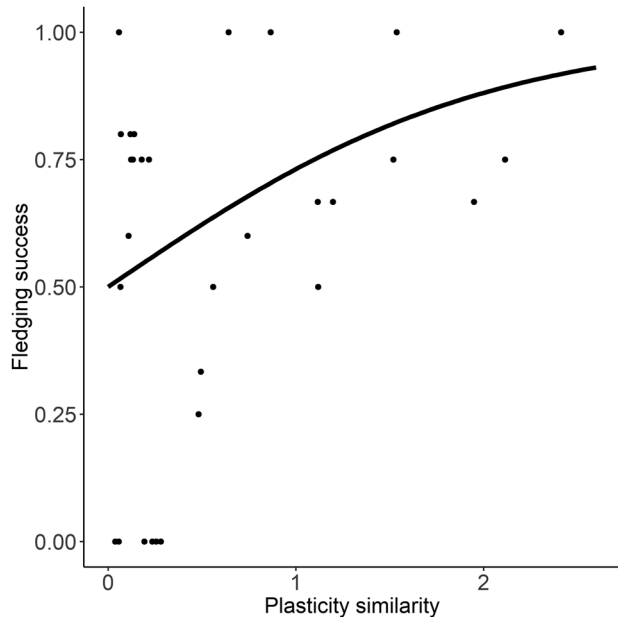
A summary of the reproductive success parameters depending on year is given in Table 2. The number of fledglings did not vary with pair boldness (NBGLMM,  $\chi^2 = 0.06$ , d.f. = 1,  $P = 0.81$ ) or boldness similarity ( $\chi^2 = 0.65$ , d.f. = 1,  $P = 0.42$ ). Fledging success did not vary with pair boldness (BGLMM,  $\chi^2 = 0.06$ , d.f. = 1,  $P = 0.81$ ) or boldness similarity ( $\chi^2 = 1.53$ ,



**Table 2.** Reproductive success parameters for Montagu's harrier pairs for each year

Reproductive success parameters	2017 ( $n = 12$ )	2018 ( $n = 6$ )	2019 ( $n = 12$ )
Number of fledglings	$1.25 \pm 1.22$ (0–3)	$3.17 \pm 0.75$ (2–4)	$2.92 \pm 1.44$ (0–5)
Fledging success	$0.38 \pm 0.37$ (0–1)	$0.77 \pm 0.19$ (0.6–1)	$0.67 \pm 0.29$ (0–1)

Values are given as the mean  $\pm$  SD (range). Sample sizes are also given for each year.



**Figure 5.** Effect of the similarity of plasticity within pairs on the fledging success (number of fledglings/number of eggs laid). The curve represents predicted values, and points indicate the observed values.

d.f. = 1,  $P = 0.22$ ). Pair plasticity influenced neither the number of fledglings ( $\chi^2 = 0.57$ , d.f. = 1,  $P = 0.45$ ) nor the fledging success ( $\chi^2 = 0.69$ , d.f. = 1,  $P = 0.41$ ). However, fledging success varied significantly depending on the plasticity similarity within pairs: it was greater for less similar pairs ( $\chi^2 = 6.57$ , d.f. = 1,  $P = 0.01$ ; Fig. 5). The number of fledglings was not impacted by plasticity similarity within pairs ( $\chi^2 = 1.73$ , d.f. = 1,  $P = 0.19$ ).

## DISCUSSION

In this study, we investigated simultaneously the pairing patterns for both boldness and plasticity and the consequences for reproductive success in a species with bi-parental care but sex-specific roles. Although our sample sizes are limited owing to our model species, the FID as a proxy for boldness was repeatable. Moreover, boldness and boldness plasticity

were correlated between males and females, revealing a positive assortative pairing pattern for both these traits. However, we failed to find evidence for any impact on the reproductive success of pairs, except for plasticity similarity within pairs, which had a negative effect on fledging success.

### FROM FLIGHT INITIATION DISTANCE TO BOLDNESS

In Montagu's harrier, the FID was repeatable across time in both sexes, reflecting consistent differences among individuals in their risk-taking behaviour, as previously shown in different species (Réale *et al.*, 2007; Bell *et al.*, 2009; Carrete & Tella, 2010; Carter *et al.*, 2012; Selmann *et al.*, 2012; Carere & Maestriperi, 2013; Møller, 2014). However, our result for females was different from the study conducted by Arroyo *et al.* (2017) on the same population, which failed to find evidence for any repeatability in FID. The first explanation for this difference could be the sample size, and thus, the statistical power. Second, some environmental conditions might have changed since 1995, such as the abundance cyclicity of the common vole (Cornulier *et al.*, 2013) or the climate, which might impact harvesting dates (Berger-Geiger *et al.*, 2019) or migration phenology (Limiñana *et al.*, 2012b, 2013). Fluctuating environmental conditions can affect the phenotypic composition of a population (Wolf & Weissing, 2010, 2012) and could explain the differences between the study by Arroyo *et al.* (2017) and ours. Further investigations are necessary to understand this discrepancy.

Although the FID was repeatable in both sexes, it was influenced by different factors. For males, the FID increased with an increase in the starting distance of the experimenter, as previously seen in other species (Blumstein, 2003, 2006; Cooper, 2005; Cooper *et al.*, 2008). When the experimenter started the approach closer to males, they flushed at a closer distance, but they did not flush directly at the start of the approach (i.e. the starting distance was not equal to FID; see Fig. 2A). Conversely, when the experimenter started the approach further away from males, they flushed at a longer distance. The starting distance was still not equal to the FID, but they did not wait for the experimenter to get closer and did not display the same FID as in the former case. An animal might

escape early to reduce the costs associated with an escape when it detects predators (Blumstein, 2006).

In contrast, Montagu's harrier females increased their FID throughout repeated approaches. This might result from the link between the rank of approaches and other factors (see Material and Methods). Indeed, female FID might increase with the nesting stage, because nestlings would become more autonomous. Another explanation could be a sensitization process, because the FID increased over repeated nest visits (sensitization process described by Blumstein, 2016; see also Rabdeau *et al.*, 2019). Furthermore, females increased their FID over time, perhaps because the number of experimenters was higher in the last approaches. The noise would be greater with a larger number of experimenters, as would the perception of predation risk, resulting in a longer FID, as also shown in crimson rosellas (*Platycercus elegans* Gmelin, 1788) (Geist *et al.*, 2005).

#### MALE AND FEMALE BOLDNESS AND PLASTICITY

Our Montagu's harrier population showed differences in boldness among individuals, with some degree of plasticity, which is in line with the concept of behavioural reaction norms (Dingemanse *et al.*, 2010). This suggests that individuals from the same population might vary in both their average behaviour (personality) and their behavioural response to changing environmental conditions (plasticity) (Dingemanse *et al.*, 2010). The fact that males did not differ from each other in their plasticity, whereas females did, could be the result of different selective pressures (Dingemanse *et al.*, 2010). For both sexes, individual boldness and plasticity were positively correlated, with shy individuals having greater plasticity than bold individuals, as shown in three-spined sticklebacks (*Gasterosteus aculeatus* Linnaeus, 1758; Jolles *et al.*, 2019). Shy individuals could be more sensitive to environmental stimuli and could thus adjust their behaviour more according to changing conditions, whereas bold individuals could be less sensitive to changes and develop routines (Koolhaas *et al.*, 1999, 2010; Kareklas *et al.*, 2016; Zidar *et al.*, 2017). These differences in behavioural plasticity are related to the adaptive character of boldness, with bold individuals experiencing better success in predictable environmental conditions, whereas shy individuals are more successful in fluctuating environmental conditions (Koolhaas *et al.*, 2010).

#### PAIRING PATTERNS FOR BOLDNESS AND PLASTICITY AND THEIR REPRODUCTIVE CONSEQUENCES

Despite our lack of statistical power owing to the small sample size, a positive assortative pairing was found

for both boldness and plasticity in our Montagu's harrier population, with a similar effect size to that found in other species, such as Steller's jay (*Cyanocitta stelleri* Gmelin, 1788; Gabriel & Black, 2012), the eastern bluebird (*Sialia sialis* Linnaeus, 1758) and African penguins (*Spheniscus demersus* Linnaeus, 1758) (Harris & Siefferman, 2014; Burtka & Grindstaff, 2015; Traisnel & Pichegru, 2017). However, the pairing pattern has not previously been assessed for plasticity traits in species with different roles in parental care. To our knowledge, our study is the first to assess the pairing pattern depending on both personality and plasticity traits in a species with sex-specific care.

Our study indicates that even with different roles of the sexes, males and females can also be associated positively for boldness and plasticity. This pattern might increase the fitness of individuals by reducing conflicts within pairs and increasing the behavioural coordination (Royle *et al.*, 2002, 2010; Both *et al.*, 2005; Schuett *et al.*, 2010, 2011; Gabriel & Black, 2012). However, only plasticity similarity within pairs influenced the fledging success in our Montagu's harrier population. Less similar pairs had higher fledging success. This result contrasts with those shown in zebra finches (Schuett *et al.*, 2011). Further investigations might consider parental investment, for example, to explore this relationship. From the present analyses, the two positive assortative pairing patterns we observed did not seem to be linked to evolutionary strategies providing fitness outcomes and thus might call into question the origin of these patterns.

#### HYPOTHESES FOR THE ORIGIN OF PAIRING PATTERNS

Assortative pairing has been studied mainly as a pattern resulting from sexual selection either through mate choice or from the post-pairing behavioural convergence of partners (Schuett *et al.*, 2010; Jiang *et al.*, 2013; Laubu *et al.*, 2016). Sexual selection would favour a positive assortative pairing if there were fitness benefits to be paired with (or converged to) a similar partner. However, in the present study, the positive assortative pairing patterns for boldness and plasticity did not provide obvious fitness benefits. Several alternative hypotheses that do not rely on sexual selection could explain these pairing patterns (reviewed by Class *et al.*, 2017; Wang *et al.*, 2019). First, assortative mating could result from sampling bias. For example, using the same experimenter to measure male and female behaviour within pairs could explain the correlations between male and female behaviour, resulting in an observer bias. However, in our study, different experimenters measured male and female behaviour, making this hypothesis unlikely. Second, temporal and/or spatial autocorrelations could occur when males and females

within pairs were measured at the same timing in their reproductive period and/or because they were exposed to the same environmental conditions (Class *et al.*, 2017). To assess whether the correlation between male and female behaviour results from temporal and/or spatial autocorrelations, an approach similar to WSC might be used (Class *et al.*, 2017; Class & Brommer, 2018; Clermont *et al.*, 2019). However, this requires all individuals to be identified in order to establish which partner they mate with each year. It also requires intensive monitoring to obtain repeated measurements on the same individuals. Although long-term monitoring data are available for the studied Montagu's harrier population (Arroyo *et al.*, 2017; Bretagnolle *et al.*, 2018), data for the same individuals for several years are unavailable in this population. The behaviour of individuals has been recorded since 1995 for females but only since 2017 for males. Moreover, most individuals were unmarked, making individual monitoring impossible from year to year. Finally, assortative pairing might result from ecological processes, owing to a non-random distribution of phenotypes in space and/or in time (Ferrer & Penteriani, 2003; Flockhart & Wiebe, 2007; Snowberg & Bolnick, 2012; Ditttrich *et al.*, 2018). In our study area, Montagu's harrier arrivals from wintering areas are spread over the breeding period (Arroyo *et al.*, 2004). This time lag could occur for different reasons, such as winter conditions or migration pathways (Limiñana *et al.*, 2012b, 2013), but might also result from differences in individual behaviour. Indeed, personality could be linked to migratory behaviour, as shown in blue tits (*Cyanistes caeruleus* Linnaeus, 1758), with migratory individuals being bolder than resident individuals (van Noordwijk *et al.*, 2006; Nilsson *et al.*, 2010, 2014). The timing of migration of Montagu's harriers could thus depend on boldness, with bold individuals migrating first, thus pairing first with available individuals that might be also bold. Additionally, spatial segregation of boldness types might also exist. Indeed, there is growing evidence for the personality-matching habitat choice hypothesis (Edelaar *et al.*, 2008; Cote *et al.*, 2010; Seltmann *et al.*, 2014; Jacob *et al.*, 2015; Zhao *et al.*, 2016; Holtmann *et al.*, 2017; Sprau & Dingemanse, 2017). Individuals could select a suitable habitat depending on their own personality. For example, in dunnocks (*Prunella modularis* Linnaeus, 1758), shy individuals settle in areas with lower human frequentation than bold individuals (Holtmann *et al.*, 2017). Consequently, the pairing pattern in Montagu's harriers might result from the spatial availability of mate phenotypes. In this case, our available long-term monitoring data on females might be used to decipher whether nesting sites are selected depending on female behaviour. Our preliminary analyses seem to

indicate that this is the case (J. Rabdeau, B. Arroyo, F. Mougeot, I. Badenhauer, V. Bretagnolle and K. Monceau, unpublished observations), thus providing a new direction for the investigation of assortative pairing in this bird species.

#### ACKNOWLEDGEMENTS

We would like to thank all the people who contributed to fieldwork: Romain Bonnet, Pierre de Bouët du Portal, Guillaume Brouard, Mélissa Desbonnes, Gildas Lemonnier, Guillaume Peplinski, Jean-Baptiste Perrotin, Margaux Ruiz, Alexis Veldeman and Alexandre Villers. We thank John A. Allen and the two anonymous reviewers for their kind reviews, which greatly improved the quality of our manuscript. We thank Catherine Menard (Direction régionale de l'Environnement, de l'Aménagement et du Logement de Nouvelle Aquitaine) for funding and administrative support. This work was supported by the Centre National de la Recherche Scientifique, the Institut National de la Recherche Agronomique and the LISEA foundation (ligne à grande vitesse Sud Europe Atlantique) for partial funding of the project 'Ressources alimentaires'. J.R. benefitted from a doctoral grant from Conseil Départemental des Deux-Sèvres, Nouvelle Aquitaine region and La Rochelle Université. The authors declare that they have no conflict of interest.

#### REFERENCES

- Ariyomo TO, Watt PJ. 2012. The effect of variation in boldness and aggressiveness on the reproductive success of zebrafish. *Animal Behaviour* **83**: 41–46.
- Arroyo BE, Bretagnolle V, Garcia JT. 2003. Land use, agricultural practices and conservation of Montagu's Harrier. In: Thompson DB, Redpath SM, Fielding AH, Galbraith CA, eds. *Birds of prey in a changing environment*. Edinburgh: Stationery Office, 449–463.
- Arroyo BE, Garcia JT, Bretagnolle V. 2002. Conservation of the Montagu's harrier (*Circus pygargus*) in agricultural areas. *Animal Conservation* **5**: 283–290.
- Arroyo BE, Garcia JT, Bretagnolle V. 2004. Montagu's Harrier. *BWP update* **6**: 41–55.
- Arroyo BE, Mougeot F, Bretagnolle V. 2017. Individual variation in behavioural responsiveness to humans leads to differences in breeding success and long-term population phenotypic changes. *Ecology Letters* **20**: 317–325.
- Bell AM, Hankison SJ, Laskowski KL. 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour* **77**: 771–783.
- Berger-Geiger B, Galizia CG, Arroyo B. 2019. Montagu's Harrier breeding parameters in relation to weather, colony size and nest protection schemes: a long-term study in Extremadura, Spain. *Journal of Ornithology* **160**: 429–441.

- Betini GS, Norris DR. 2012.** The relationship between personality and plasticity in tree swallow aggression and the consequences for reproductive success. *Animal Behaviour* **83**: 137–143.
- Bitton P-P, Dawson RD, Ochs CL. 2008.** Plumage characteristics, reproductive investment and assortative mating in tree swallows *Tachycineta bicolor*. *Behavioral Ecology and Sociobiology* **62**: 1543–1550.
- Black JM, Owen M. 1995.** Reproductive performance and assortative pairing in relation to age in barnacle geese. *Journal of Animal Ecology* **64**: 234–244.
- Blumstein DT. 2003.** Flight-initiation distance in birds is dependent on intruder starting distance. *Journal of Wildlife Management* **67**: 852–857.
- Blumstein DT. 2006.** Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Animal Behaviour* **71**: 389–399.
- Blumstein DT. 2016.** Habituation and sensitization: new thoughts about old ideas. *Animal Behaviour* **120**: 255–262.
- Bolker B, Skaug H, Magnusson A, Nielsen, A. 2012.** *Getting started with the glmmADMB package*.
- Bonneaud C, Chastel O, Federici P, Westerdahl H, Sorci G. 2006.** Complex *Mhc*-based mate choice in a wild passerine. *Proceedings of the Royal Society B: Biological Sciences* **273**: 1111–1116.
- Both C, Dingemanse NJ, Drent PJ, Tinbergen JM. 2005.** Pairs of extreme avian personalities have highest reproductive success. *Journal of Animal Ecology* **74**: 667–674.
- Bretagnolle V, Berthet E, Gross N, Gauffre B, Plumejeaud C, Houte S, Badenhauer I, Monceau K, Allier F, Monestiez P, Gaba S. 2018.** Towards sustainable and multifunctional agriculture in farmland landscapes: Lessons from the integrative approach of a French LTSER platform. *Science of the Total Environment* **627**: 822–834.
- Burtka JL, Grindstaff JL. 2015.** Similar nest defence strategies within pairs increase reproductive success in the eastern bluebird, *Sialia sialis*. *Animal Behaviour* **100**: 174–182.
- Butet A, Leroux ABA. 2001.** Effects of agriculture development on vole dynamics and conservation of Montagu's harrier in western French wetlands. *Biological Conservation* **100**: 289–295.
- Carere C, Maestriperi D. 2013.** *Animal personalities: behavior, physiology, and evolution*. Chicago: Chicago University Press.
- Carrete M, Tella JL. 2010.** Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance-induced habitat selection. *Biological Letters* **6**: 167–170.
- Carter A, Goldizen A, Heinsohn R. 2012.** Personality and plasticity: temporal behavioural reaction norms in a lizard, the Namibian rock agama. *Animal Behaviour* **84**: 471–477.
- Chadœuf J, Millon A, Bourrioux JL, Printemps T, Van Hecke B, Lecoustre V, Bretagnolle V. 2018.** Modelling unbiased dispersal kernels over continuous space by accounting for spatial heterogeneity in marking and observation efforts. *Methods in Ecology and Evolution* **9**: 331–339.
- Champely S, Ekstrom C, Dalgaard P, Gill J, Weibelzahl S, Anandkumar A, Ford C, Volcic R, De Rosario MH. 2018.** Package 'pwr'. Available from: <http://cran.r-project.org/package=pwr>
- Class B, Brommer JE. 2018.** Shared environmental effects bias phenotypic estimates of assortative mating in a wild bird. *Biological Letters* **14**: 20180106.
- Class B, Dingemanse NJ, Araya-Ajoy YG, Brommer JE. 2017.** A statistical methodology for estimating assortative mating for phenotypic traits that are labile or measured with error. *Methods in Ecology and Evolution* **8**: 1910–1919.
- Clermont J, Réale D, Giroux J-F. 2019.** Similarity in nest defense intensity in Canada goose pairs. *Behavioral Ecology Sociobiology* **73**: 108.
- Cohen J. 1988.** *Statistical power analysis for the behavioral sciences, 2nd edn*. Hillsdale: Lawrence Erlbaum Associates.
- Cooper WE Jr. 2005.** When and how do predator starting distances affect flight initiation distances? *Canadian Journal of Zoology* **83**: 1045–1050.
- Cooper WE, Attum O, Kingsbury B. 2008.** Escape behaviors and flight initiation distance in the common water snake *Nerodia sipedon*. *Journal of Herpetology* **42**: 493–500.
- Cornulier T, Yoccoz NG, Bretagnolle V, Brommer JE, Butet A, Ecke F, Elston DA, Framstad E, Henttonen H, Hörnfeldt B, Huitu O, Imholt C, Ims RA, Jacob J, Jędrzejewska B, Millon A, Petty SJ, Pietiäinen H, Tkadlec E, Zub K, Lambin X. 2013.** Europe-wide dampening of population cycles in keystone herbivores. *Science* **340**: 63–66.
- Cote J, Clobert J, Brodin T, Fogarty S, Sih A. 2010.** Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**: 4065–4076.
- Crawley MJ. 2012.** *The R book*. Chichester: Wiley Publishing.
- Daunt F, Monaghan P, Wanless S, Harris MP. 2003.** Sexual ornament size and breeding performance in female and male European shags *Phalacrocorax aristotelis*. *Ibis* **145**: 54–60.
- Dingemanse NJ, Bouwman KM, van de Pol M, van Overveldt T, Patrick SC, Matthysen E, Quinn JL. 2012.** Variation in personality and behavioural plasticity across four populations of the great tit *Parus major*. *Journal of Animal Ecology* **81**: 116–126.
- Dingemanse NJ, Kazem AJN, Réale D, Wright J. 2010.** Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution* **25**: 81–89.
- Dittrich C, Rodríguez A, Segev O, Drakulić S, Feldhaar H, Vences M, Rödel MO. 2018.** Temporal migration patterns and mating tactics influence size-assortative mating in *Rana temporaria*. *Behavioral Ecology* **29**: 418–428.
- Edelaar P, Siepielski AM, Clobert J. 2008.** Matching habitat choice causes directed gene flow: a neglected dimension in evolution and ecology. *Evolution* **62**: 2462–2472.
- Favre B, Prévault M, Théry M, Secondi J, Patris B, Cézilly F. 2001.** Breeding strategy and morphological characters in an urban population of blackbirds, *Turdus merula*. *Animal Behaviour* **5**: 969–974.

- Fargevieille A, Grégoire A, Charmantier A, del Rey Granado M, Doutrelant C. 2017.** Assortative mating by colored ornaments in blue tits: space and time matter. *Ecology and Evolution* **7**: 2069–2078.
- Ferrer M, Penteriani V. 2003.** A process of pair formation leading to assortative mating: passive age-assortative mating by habitat heterogeneity. *Animal Behaviour* **66**: 137–143.
- Flockhart DT, Wiebe KL. 2007.** The role of weather and migration in assortative pairing within the northern flicker (*Colaptes auratus*) hybrid zone. *Evolutionary Ecology Research* **9**: 887–903.
- Fox J, Weisberg S. 2011.** *An R companion to applied regression, 2nd edn.* Thousand Oaks: Sage Publications.
- Fox J, Weisberg S, Bates D, Fox MJ. 2012.** Package “car”. Available from: <http://cran.r-project.org/web/packages/car/car.pdf>
- Frid A, Dill L. 2002.** Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* **6**: 11–26.
- Gabriel PO, Black JM. 2012.** Behavioural syndromes, partner compatibility and reproductive performance in Steller’s jays. *Ethology* **118**: 76–86.
- García JT, Arroyo BE. 2001.** Effect of abiotic factors on reproduction in the centre and periphery of breeding ranges: a comparative analysis in sympatric harriers. *Ecography* **24**: 393–402.
- Geist C, Liao J, Libby S, Blumstein DT. 2005.** Does intruder group size and orientation affect flight initiation distance in birds? *Animal Biodiversity and Conservation* **28**: 69–73.
- Harris MR, Siefferman L. 2014.** Interspecific competition influences fitness benefits of assortative mating for territorial aggression in eastern bluebirds (*Sialia sialis*). *PLoS One* **9**: e88668.
- Holtmann B, Santos ESA, Lara CE, Nakagawa S. 2017.** Personality-matching habitat choice, rather than behavioural plasticity, is a likely driver of a phenotype–environment covariance. *Proceedings of the Royal Society B: Biological Sciences* **284**: 20170943.
- Ihle M, Kempenaers B, Forstmeier W. 2015.** Fitness benefits of mate choice for compatibility in a socially monogamous species. *PLoS Biology* **13**: e1002248.
- Jacob S, Bestion E, Legrand D, Clobert J, Cote J. 2015.** Habitat matching and spatial heterogeneity of phenotypes: implications for metapopulation and metacommunity functioning. *Evolutionary Ecology* **29**: 851–871.
- Jiang Y, Bolnick DI, Kirkpatrick M. 2013.** Assortative mating in animals. *The American Naturalist* **181**: E125–E138.
- Jolles JW, Briggs HD, Araya-Ajoy YG, Boogert NJ. 2019.** Personality, plasticity and predictability in sticklebacks: bold fish are less plastic and more predictable than shy fish. *Animal Behaviour* **154**: 193–202.
- Kareklas K, Arnott G, Elwood RW, Holland RA. 2016.** Plasticity varies with boldness in a weakly-electric fish. *Frontiers in Zoology* **13**: 22.
- Kontiainen P, Pietiäinen H, Huttunen K, Karell P, Kolunen H, Brommer JE. 2009.** Aggressive Ural owl mothers recruit more offspring. *Behavioral Ecology* **20**: 789–796.
- Koolhaas JM, de Boer SF, Coppens CM, Buwalda B. 2010.** Neuroendocrinology of coping styles: Towards understanding the biology of individual variation. *Frontiers in Neuroendocrinology* **31**: 307–321.
- Koolhaas JM, Korte SM, de Boer SF, van der Vegt BJ, van Reenen CG, Hopster H, de Jong IC, Ruis MAW, Blokhuis HJ. 1999.** Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews* **23**: 925–935.
- Kuznetsova A, Brockhoff PB, Christense RHB. 2014.** Tests for random and fixed effects for linear mixed effect models (lmer objects of lme 4 package). Available from: <http://CRAN.R-project.org/package=lmerTest>
- Laubu C, Dechaume-Moncharmont FX, Motreuil S, Schweitzer C. 2016.** Mismatched partners that achieve postpairing behavioral similarity improve their reproductive success. *Science Advances* **2**: e1501013.
- Limiñana R, García JT, González JM, Guerrero Á, Lavedán J, Moreno JD, Román-Muñoz A, Palomares LE, Pinilla A, Ros G, Serrano C, Surroca M, Tena J, Arroyo BE. 2012a.** Philopatry and natal dispersal of Montagu’s harriers (*Circus pygargus*) breeding in Spain: a review of existing data. *European Journal of Wildlife Research* **58**: 549–555.
- Limiñana R, Romero M, Mellone U, Urios V. 2013.** Is there a different response to winds during migration between soaring and flapping raptors? An example with the Montagu’s harrier and the lesser kestrel. *Behavioral Ecology and Sociobiology* **67**: 823–835.
- Limiñana R, Soutullo A, Urios V, Reig-Ferrer A. 2012b.** Migration and wintering areas of adult Montagu’s Harriers (*Circus pygargus*) breeding in Spain. *Journal of Ornithology* **153**: 85–93.
- Ludwig SC, Becker PH. 2008.** Supply and demand: causes and consequences of assortative mating in common terns *Sterna hirundo*. *Behavioral Ecology and Sociobiology* **62**: 1601–1611.
- MacDougall AK, Montgomerie R. 2003.** Assortative mating by carotenoid-based plumage colour: a quality indicator in American goldfinches, *Carduelis tristis*. *Naturwissenschaften* **90**: 464–467.
- Masello JF, Quillfeldt P. 2003.** Body size, body condition and ornamental feathers of Burrowing Parrots: variation between years and sexes, assortative mating and influences on breeding success. *Emu* **103**: 149–161.
- Masumoto T. 1999.** Size assortative mating and reproductive success of the funnel-web spider, *Agelena limbata* (Araneae: Agelenidae). *Journal of Insect Behavior* **12**: 353–361.
- Millon A, Arroyo BE, Bretagnolle V. 2008.** Variable but predictable prey availability affects predator breeding success: natural versus experimental evidence. *Journal of Zoology* **275**: 349–358.
- Millon A, Bourrioux JL, Riols C, Bretagnolle V. 2002.** Comparative breeding biology of Hen Harrier and Montagu’s Harrier: an 8-year study in north-eastern France. *Ibis* **144**: 94–105.

- Millon A, Bretagnolle V. 2008.** Predator population dynamics under a cyclic prey regime: numerical responses, demographic parameters and growth rates. *Oikos* **117**: 1500–1510.
- Møller AP. 2014.** Life history, predation and flight initiation distance in a migratory bird. *Journal of Evolutionary Biology* **27**: 1105–1113.
- Møller AP, Vágási CI, Pap PL. 2013.** Risk-taking and the evolution of mechanisms for rapid escape from predators. *Journal of Evolutionary Biology* **26**: 1143–1150.
- Montiglio P-O, Wey TW, Chang AT, Fogarty S, Sih A. 2016.** Multiple mating reveals complex patterns of assortative mating by personality and body size. *Journal of Animal Ecology* **85**: 125–135.
- Mougeot F, Arroyo BE, Bretagnolle V. 2001.** Decoy presentations as a means to manipulate the risk of extrapair copulation: an experimental study in a semicolonial raptor, the Montagu's harrier (*Circus pygargus*). *Behavioral Ecology* **12**: 1–7.
- Mougeot F, Arroyo BE, Bretagnolle V. 2006.** Paternity assurance responses to first-year and adult male territorial intrusions in a courtship-feeding raptor. *Animal Behaviour* **71**: 101–108.
- Nakagawa S, Cuthill IC. 2007.** Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews* **82**: 591–605.
- Nakagawa S, Schielzeth H. 2010.** Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews* **85**: 935–956.
- Nilsson ALK, Nilsson J-Å, Alerstam T, Bäckman J. 2010.** Migratory and resident blue tits *Cyanistes caeruleus* differ in their reaction to a novel object. *Naturwissenschaften* **97**: 981–985.
- Nilsson J-Å, Bronmark C, Hansson LA, Chapman BB. 2014.** Individuality in movement: the role of personality. In: Hansson L-A, Akesson S, eds. *Animal movement across scales*. Oxford: Oxford University Press, 90–109.
- van Noordwijk AJ, Pulido F, Helm B, Coppack T, Delingat J, Dingle H, Hedenström A, van der Jeugd H, Marchetti C, Nilsson A, Pérez-Tris J. 2006.** A framework for the study of genetic variation in migratory behaviour. *Journal of Ornithology* **147**: 221–233.
- Nussey DH, Wilson AJ, Brommer JE. 2007.** The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology* **20**: 831–844.
- Ortego J, Calabuig G, Bonal R, Muñoz A, Aparicio JM, Cordero PJ. 2009.** Temporal variation of heterozygosity-based assortative mating and related benefits in a lesser kestrel population. *Journal of Evolutionary Biology* **22**: 2488–2495.
- Pack AA, Herman LM, Spitz SS, Craig AS, Hakala S, Deakos MH, Herman EYK, Milette AJ, Carroll E, Levitt S, Lowe C. 2012.** Size-assortative pairing and discrimination of potential mates by humpback whales in the Hawaiian breeding grounds. *Animal Behaviour* **84**: 983–993.
- Pérez i de Lanuza G, Font E, Carazo P. 2013.** Color-assortative mating in a color-polymorphic lacertid lizard. *Behavioral Ecology* **24**: 273–279.
- van de Pol M, Wright J. 2009.** A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behaviour* **77**: 753–758.
- R Core Team. 2018.** *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Rabdeau J, Badenhauer I, Moreau J, Bretagnolle V, Monceau K. 2019.** To change or not to change experimenters: caveats for repeated behavioural and physiological measures in Montagu's harrier. *Journal of Avian Biology* **50**: e02160.
- Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007.** Integrating animal temperament within ecology and evolution. *Biological Reviews* **82**: 291–318.
- Royle NJ, Hartley IR, Parker GA. 2002.** Sexual conflict reduces offspring fitness in zebra finches. *Nature* **416**: 733–736.
- Royle NJ, Schuett W, Dall SRX. 2010.** Behavioral consistency and the resolution of sexual conflict over parental investment. *Behavioral Ecology* **21**: 1125–1130.
- Santangeli A, Arroyo BE, Millon A, Bretagnolle V. 2015.** Identifying effective actions to guide volunteer-based and nationwide conservation efforts for a ground-nesting farmland bird. *Journal of Applied Ecology* **52**: 1082–1091.
- Schuett W, Dall SRX, Royle NJ. 2011.** Pairs of zebra finches with similar 'personalities' make better parents. *Animal Behaviour* **81**: 609–618.
- Schuett W, Tregenza T, Dall SRX. 2010.** Sexual selection and animal personality. *Biological Reviews* **85**: 217–246.
- Seltmann MW, Jaatinen K, Steele BB, Öst M. 2014.** Boldness and stress responsiveness as drivers of nest-site selection in a ground-nesting bird. *Ethology* **120**: 77–89.
- Seltmann MW, Öst M, Jaatinen K, Atkinson S, Mashburn K, Hollmén T. 2012.** Stress responsiveness, age and body condition interactively affect flight initiation distance in breeding female eiders. *Animal Behaviour* **84**: 889–896.
- Servedio MR, Boughman JW. 2017.** The role of sexual selection in local adaptation and speciation. *Annual Review of Ecology, Evolution, and Systematics* **48**: 85–109.
- da Silva Castiglioni D, Bond-Buckup G. 2008.** Pairing and reproductive success in two sympatric species of *Hyalella* (Crustacea, Amphipoda, Dogielinotidae) from southern Brazil. *Acta Oecologica* **33**: 49–55.
- Snowberg LK, Bolnick DI. 2012.** Partitioning the effects of spatial isolation, nest habitat, and individual diet in causing assortative mating within a population of threespine stickleback. *Evolution* **66**: 3582–3594.
- Spoon TR, Millam JR, Owings DH. 2006.** The importance of mate behavioural compatibility in parenting and reproductive success by cockatiels, *Nymphicus hollandicus*. *Animal Behaviour* **71**: 315–326.
- Sprau P, Dingemanse NJ. 2017.** An approach to distinguish between plasticity and non-random distributions of behavioral types along urban gradients in a wild passerine bird. *Frontiers in Ecology and the Environment* **5**: 92.

- Traisnel G, Pichegru L. 2017.** Does it always pay to defend one's nest? A case study in African penguin. *Ethology* **124**: 74–83.
- Wang D, Forstmeier W, Valcu M, Dingemanse N, Bulla M, Both C, Duckworth RA, Kiere LM, Karell P, Albrecht T, Kempenaers B. 2019.** Scrutinizing assortative mating in birds. *PLoS Biology* **17**: e3000156.
- Wolf M, Weissing FJ. 2010.** An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**: 3959–3968.
- Wolf M, Weissing FJ. 2012.** Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution* **27**: 452–461.
- Zhao Q-S, Hu Y-B, Liu P-F, Chen L-J, Sun Y-H. 2016.** Nest site choice: a potential pathway linking personality and reproductive success. *Animal Behaviour* **118**: 97–103.
- Zidar J, Balogh A, Favati A, Jensen P, Leimar O, Lovlie H. 2017.** A comparison of animal personality and coping styles in the red junglefowl. *Animal Behaviour* **130**: 209–220.

### SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Appendix S1.** Power analyses for Spearman's rank correlation tests.

**Table S1.** Power analysis results for Spearman's rank correlation tests ( $\rho$ ) examining the links between male and female boldness and plasticity. Power analyses were conducted for all years pooled and for each year separately (2017, 12 pairs; 2018, six pairs; and 2019, 12 pairs).