

RESEARCH ARTICLE

Sexual selection and personality: Individual and group-level effects on mating behaviour in red junglefowl

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Handling Editor: Beatriz Willink

Abstract

1. Despite increasing evidence of the importance of repeatable among-individual differences in behaviour (animal personality) in ecology and evolution, little remains known about the role of animal personalities in sexual selection.
2. Here, we present an investigation of the hypothesis that the personalities of individuals and their sexual partners play a role in different episodes of sexual selection, and the extent to which these effects are modulated by the social environment.
3. We first examined how two repeatable behaviours—exploration and boldness—are associated with pre- and postcopulatory sexual selection in male red junglefowl *Gallus gallus*, using replicate groups across three experimental sex ratio treatments. We further explored how the social environment modulates relationships between male personality and mating performance, and whether mating is assortative or disassortative with respect to exploration or boldness. Finally, we examined behavioural mechanisms linking personality with mating performance.
4. Across all sex ratios, the fastest and slowest exploring males courted females proportionally less, and faster exploring males associated with females more and received more sexual solicitations. In female-biased groups, the fastest and slowest exploring males experienced the highest mating success and lowest sperm competition intensity. Faster exploring males also obtained more mates in female-biased groups when their competitors were, on average, slower exploring, and the proportion of matings obtained by fast-exploring males decreased with the proportion of fast-exploring males in a group, consistent with negative frequency-dependent sexual selection. While boldness did not predict mating performance,

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there was a tendency for individuals to mate disassortatively with respect to boldness.

5. Collectively, our results suggest that male exploration can play a role in sexual selection, and that sexual selection on personality is complex and contingent on the social environment.

KEYWORDS

boldness, disassortative mating, exploration, group phenotypic composition, negative frequency dependence, social selection

1 | INTRODUCTION

A wide range of animal species show repeatable among-individual variation in behaviours such as exploration, boldness and aggression, a pattern known as animal personality (Carere & Maestripieri, 2013; Dall et al., 2004; Dingemanse et al., 2010; Durkin et al., 2020; Sih, Bell & Johnson, 2004). Personality can have fitness consequences via effects on survival and/or reproduction (reviewed in Dingemanse & Réale, 2005; Moiron et al., 2020; Réale & Dingemanse, 2010; Réale et al., 2007; Royauté et al., 2018; Smith & Blumstein, 2008) and often displays a considerable additive genetic component (reviewed in Dochtermann et al., 2015; Sommer-Trembo et al., 2016; van Oers et al., 2005). A major focus of research is therefore to understand patterns of selection on personality and the mechanisms that maintain interindividual variation in behaviour. Evolutionary responses to selection depend on the extent to which different repeatable behavioural traits are correlated across individuals, forming a behavioural syndrome (e.g. Bell & Sih, 2007; Dingemanse et al., 2007; Moiron et al., 2019; Verbeek et al., 1994; Verbeek et al., 1996). While patterns of selection on animal personality have attracted increasing research interest (Dall et al., 2004; Dingemanse et al., 2010; Dochtermann et al., 2015; Sih, Bell & Johnson, 2004; Sommer-Trembo et al., 2016), little remains known about the relationship between sexual selection and personality (Munson et al., 2020; Schuett et al., 2010; Tuni et al., 2018).

Sexual selection arises from differential reproductive success among members of the same sex, caused by competition over access to reproductive partners and their gametes (Andersson, 1994; Darwin, 1871). In males, where intrasexual competition is typically more intense (Janicke et al., 2016; Kokko et al., 2006), variation in reproductive success is governed by precopulatory mechanisms determining the number of females mated (i.e. mating success) and the fecundity of those females. In species where females mate with multiple males (polyandry), variation between males in reproductive performance is also governed by postcopulatory mechanisms determining the proportion of eggs that a male fertilizes via sperm competition (Parker, 1970; Parker & Birkhead, 2013) and cryptic female choice (Eberhard, 1996; Firman et al., 2017). Sexual selection may favour males with personality types associated with certain behaviours or physiological responses (Cockrem, 2007; Reaney & Backwell, 2007; Verbeek et al., 1999) if these behaviours influence

a male's access to mates via intrasexual competition (Colléter & Brown, 2011; Schuett et al., 2010) or influence a male's reproductive success via intersexual attraction (Dziweczynski et al., 2013; Godin & Dugatkin, 1996; Munson et al., 2020; Reaney & Backwell, 2007; Schuett et al., 2010, 2011; Teyssier et al., 2014). The evolution of female preferences for male personalities could, in principle, be explained if personality-related behaviours are costly (Biro & Stamps, 2010) or more risky, making personality an indicator of a male's breeding value for viability and/or parental ability (Munson et al., 2020; Schuett et al., 2010; Tuni et al., 2018). Similarly, female personality may play a key role in sexual selection on male personality, by influencing female responses to males (Munson et al., 2020). Interactions between male and female personality may also influence a male's reproductive success if females prefer males that are behaviourally similar to themselves, leading to assortative mating (Montiglio et al., 2016; Munson et al., 2020; Schuett et al., 2010, 2011). Choosing a behaviourally similar mate may confer advantages, if similar pairs are better able to coordinate parental activities such as food provisioning and nest defence (Munson et al., 2020; Schuett et al., 2010). Alternatively, females may prefer mates that are behaviourally dissimilar to themselves, promoting disassortative mating (Both et al., 2005; Dingemanse et al., 2004; Montiglio et al., 2016; Munson et al., 2020; van Oers et al., 2008). Dissimilar pairings may be advantageous if offspring with intermediate phenotypes are more viable than offspring with extreme phenotypes or if similar pairs are genetically or behaviourally incompatible (Dingemanse et al., 2004; Schuett et al., 2010). Nevertheless, the majority of past work examining assortative mating for labile traits fails to consider that processes such as the convergence of phenotypes between mates after mating, scale of choice effects, shared environmental responses and/or correlated measurement error may cause apparent non-random assortment to arise (Class et al., 2017; Dingemanse et al., 2020; Munson et al., 2020). Thus, we have limited empirical knowledge about whether assortative mating occurs with respect to personality.

In polyandrous species, personality may also influence postcopulatory sexual selection (Bridger et al., 2015; Gasparini et al., 2019; Herdegen-Radwan, 2019; Tuni et al., 2018). Male personality, female personality or their interaction could affect a male's paternity share by modulating the degree of female polyandry and the outcome of sperm competition, for example, by determining how long or how

often pairs mate. In a population of socially monogamous great tits *Parus major*, males that were, on average, more aggressive and explorative gained a lower share of extra-pair paternity (Araya-Ajoy et al., 2016; but see Patrick et al., 2011; Roth et al. 2019). In the more promiscuous field cricket *Gryllus bimaculatus*, on the other hand, consistently more aggressive males may be favoured in postcopulatory sexual selection (Tuni et al., 2018).

Because it is a form of social selection (Lyon & Montgomerie, 2012), sexual selection is likely to be sensitive to variation in the social environment. First, the sex ratio of an individual's social environment is predicted to influence the intensity and mechanisms of pre- and postcopulatory sexual selection (Bleu et al., 2012; Emlen & Oring, 1977; Kvarnemo & Simmons, 2013; but see Pröhl, 2002; Wey et al., 2015) and the relationship between pre- and postcopulatory competition (Wey et al., 2015). Adult or operational sex ratio could therefore play an important role in determining the relationship between male personality and male reproductive success by modulating selection pressures (Del Giudice, 2012; Pröhl, 2002; Weir et al., 2011; Wey et al., 2015). Second, the phenotypic composition of an individual's social environment may have critical repercussions on patterns of selection on personality. Group phenotypic composition refers to any descriptor of the phenotypic make-up of a group (which may be defined at various levels, from a pair to an entire community), such as the mean, variance or presence of an extreme phenotype (Farine et al., 2015), and several studies have demonstrated a link between individual fitness and group personality composition (Sih & Watters, 2005; Sih et al., 2014; Wey et al., 2015, but see Roth et al., 2019). In addition to influencing the strength or directionality of sexual selection, the social environment may also modulate the shape of sexual selection on personality. For example, in water striders *Aquarius remigis*, directional selection for more aggressive males is observed in closed populations, while sexual selection for male aggression has a negative quadratic shape in open populations, where the connectivity between populations allows for shifts in the phenotypic distribution in local pools, as females can move away from persistent male harassment (Eldakar et al., 2009; Eldakar, Dlugos, et al., 2010; Eldakar, Wilson, et al., 2010; Sih et al., 2014). Importantly, group personality composition could interact with the personality of focal individuals, with focal individuals having higher fitness when competitors are, on average, either similar (i.e. positive frequency-dependent selection) or dissimilar (i.e. negative frequency-dependent selection; Dall et al., 2004) in personality. Little, however, is known about the way in which pre- and postcopulatory sexual selection target male personality at both individual and group levels.

Here, we use an experimental approach to examine the role of two behavioural traits, exploration and boldness, in patterns of sexual selection in male red junglefowl *Gallus gallus*. There is evidence of personality in populations of red junglefowl, as well as in populations of the closely related domestic fowl *G. domesticus*, with several traits showing individual repeatability, including exploration, boldness and aggression (Favati et al., 2014, 2016, 2017, 2018; Favati et al., 2014; Zidar et al., 2017, 2018). In nature, red junglefowl live

in small groups and form sex-specific social hierarchies (Collias & Collias, 1996; Collias et al., 1994; Kim & Zuk, 2000; Lill, 1966; Pizzari & McDonald, 2019; Thornhill, 1988). Social status plays an important role in mediating the outcome of intrasexual competition and can influence mating success in both males and females (Collias & Collias, 1996; Collias et al., 1994; Kim & Zuk, 2000; Lill, 1966; Pizzari & McDonald, 2019; Thornhill, 1988). In principle, male personality may affect male reproductive success indirectly, by influencing male social status, or directly (i.e. independently of male social status). Faster exploring male fowl have been shown to be more likely to defeat slower exploring competitors in dyadic contests, but neither exploration nor boldness has been found to predict social rank in a group setting (Favati, Leimar, & Løvlie, 2014; Favati et al., 2017). Similarly, female personality may affect polyandry indirectly through an influence on female social status, or directly (i.e. independently of female social status).

Sexual behaviour in fowl is strongly modulated by the social environment (Pizzari & McDonald, 2019). Prior studies of natural or semi-natural populations of red junglefowl have demonstrated that groups may comprise two to 20 individuals and exhibit sex ratios ranging from all male to mostly female (e.g. c. 78% female; Collias & Collias, 1967, 1996; Javed & Rahmani, 2000). In male-biased groups, matings are often male-initiated, male sexual harassment of females can be intense and male social status may have limited influence on mate monopolization, resulting in high levels of polyandry and opportunity for postcopulatory sexual selection (Løvlie & Pizzari, 2007). Conversely, in groups with a strong female bias, females are more proactive in soliciting matings from preferred males and male social status can play a prominent role in mate monopolization, generating opportunity for precopulatory sexual selection, while limiting polyandry and opportunity for postcopulatory sexual selection (Løvlie & Pizzari, 2007; Pizzari & McDonald, 2019). Moreover, previous work has demonstrated a positive covariance between male performance in pre- and postcopulatory selection in weakly female-biased groups, indicating that socially dominant, aggressive males are favoured, both before and after mating (Collet et al., 2012; McDonald et al., 2017). This relationship emerges as a result of these males being able to mate with more females (higher mating success) and remate with these females more frequently, thus achieving a higher share of paternity. This effect is consistent with previous artificial insemination studies demonstrating that fertilizing advantage is determined by the relative number of sperm inseminated by competing males, particularly in the short term, following insemination (Martin et al., 1974; Pizzari et al., 2008). In addition to remating frequently with a female, a male's paternity share in freely mating groups is increased when a male is able to mate last with a female, when the female is less polyandrous and when his advances are not resisted by the female (Carleial et al., 2020).

We measured exploration and boldness for male and female red junglefowl and studied their mating behaviour across 24 replicate groups under three sex ratios: male-biased, even and female-biased. We first focused on precopulatory sexual selection and investigated the role of male personality and the personality composition of his

competitors, in male mating success. Second, we examined postcopulatory sexual selection and tested whether female personality affects the degree of polyandry and assessed the relative importance of a focal male's personality and male competitor personality composition on the levels of sperm competition intensity (SCI) suffered by individual males, as well as a male's rate of remating with individual females. Third, we tested whether individuals mated assortatively with respect to personality type. Finally, we considered the behavioural mechanisms underpinning differential mating patterns by investigating the role of personality in male courting of females, tendency to associate with females and female solicitation of males.

The patterns explored are potentially complex, which makes it difficult to generate clear *a priori* predictions, and thus, a key role of our study is to provide a quantitative basis for generating future hypotheses. Nevertheless, we hypothesized that pre- and postcopulatory sexual selection would target male personality in a similar way, and we predicted that faster exploring and/or bolder males would attain more mates, have higher rates of remating with the same females and experience lower levels of sperm competition. We further hypothesized that female behaviour would play a role in sexual selection on male personality. We considered a scenario in which all females in a group would, on average, bias mating towards faster exploring and/or bolder males, and an assortative/disassortative scenario in which females preferentially mate with males having personalities similar or dissimilar to their own. Furthermore, we hypothesized that the social environment would influence patterns of sexual selection on male personality. We expected sexual selection on male personality to be stronger in male-biased, compared to female-biased, groups, if male personality is associated with success in intrasexual competition, particularly with respect to sperm competition. Conversely, if male personality determines precopulatory female preference, we expected sexual selection on male personality to be relatively strong in female-biased groups. Potentially antagonistic interactions between intra- and intersexual or between pre- and postcopulatory mechanisms may also contribute to nonlinear patterns of sexual selection on male personality, particularly in groups with even sex ratios (which offer considerable opportunity for both pre- and postcopulatory sexual selection) and female-biased groups (where females have more opportunity to exercise their preference). Finally, we considered a scenario in which males fare worse in groups composed primarily of faster exploring and/or bolder males, and a negative frequency-dependent scenario, in which males of a given personality type perform worse with increasing frequency of competitors of similar personality type.

2 | MATERIALS AND METHODS

2.1 | Study system

We studied a captive population of red junglefowl housed at the John Krebs Field Station in Wytham, UK. All birds were individually ringed with numbered Darvic rings to facilitate identification and were sexually mature, ranging from 1 to 10 years of age. Overall, we

studied personality in 56 males and 38 females. All work was carried out according to United Kingdom home office legislation (Home office license 30/2418), following approval by the Departmental Animal Welfare Ethical Review Body (AWERB).

We exposed individuals to two behavioural assays: (a) a novel arena test to investigate exploration (i.e. locomotion in a novel environment) and (b) a novel object test to investigate boldness (i.e. propensity to approach and feed in the presence of a novel object). Exploration and boldness have been examined previously in fowl using a similar protocol and have been found to vary among individuals (Favati, Leimar, & Løvlie, 2014; Favati et al., 2016; Zidar et al., 2017). Both assays were modified from the methods described in Zidar et al. (2017), and our methods yielded repeatable measures (see Appendix S1 for further details).

We created 24 groups, each comprising 12 individuals, of three different sex ratios: eight male-biased groups (9 males: 3 females), eight even sex ratio groups (6:6) and eight female-biased groups (3:9). We studied 12 groups in May–August 2016 and 12 additional groups in April–July 2017. In the first breeding season, we started by observing four even sex ratio groups, followed by four male-biased groups, and we concluded the year by observing four female-biased groups. In the second breeding season, we randomized the order of groups with different sex ratios to control for potential seasonal effects on behaviour. All groups were housed and studied in a $11.5 \times 7.2 \text{ m}^2$ outdoor pen. We experimentally manipulated the exploration composition of males and females in the groups, based on the mean values of the first two novel arena trials, so that both male and female group means ranged from faster to slower exploring within each sex ratio. Because exploration and boldness scores were orthogonal (see Section 3), we pragmatically decided to only manipulate group exploration composition and allowed variation in group boldness composition to vary unsystematically. For mating trials, male age ranged from 3 to 9 years ($M \pm SD = 4.25 \pm 1.49$ years), while female age ranged from 1 to 9 years ($M \pm SD = 3.75 \pm 2.11$ years). For each group, we placed males in the pen at c. 1:00 p.m. local time and gave them 24 hr to establish a social hierarchy before introducing females to the pen at c. 1:00 p.m. the following day. We conducted 3-hr behavioural observations on each group, for six evenings (3 hr before sunset to sunset, local time) and five mornings (sunrise to 3 hr after sunrise, local time), for a total of 33 observation hours per group, starting the evening of the day that females were introduced. We recorded all same-sex dominance interactions (chases, lunges, aggressive pecking, active avoidances and fights), female solicitations of mating, male to female waltzing, male sexual harassment of females, and heterosexual mating attempts. We scored mating attempts as successful or unsuccessful. Successful matings were defined as attempts in which a male mounted a female, lowered his train and cloacal contact was observed or assumed to have occurred (see Løvlie & Pizzari, 2007). A female was considered to have solicited when she initiated mating by crouching in front of a male (Etches, 1996; Løvlie et al., 2005; Løvlie & Pizzari, 2007; Pizzari, 2001). For all same-sex dominance interactions, we recorded the winning and losing individual; for all other interactions, we recorded the actor and receiver. Fights sometimes ended in a stalemate, and we recorded the

outcome of these interactions as 'draws'. We also conducted scan samples every 30 min and recorded all individuals who were within one body length of each other. A total of 77 scan samples were recorded for each of 24 groups.

2.2 | Statistical methods

2.2.1 | Social hierarchies

We used R 3.3.2 for all analyses (R Core Team, 2018). We used all same-sex dyadic dominance interactions, with the exception of fights that ended in a draw, to analyse sex-specific social hierarchies. Using the number of interactions won versus lost for each individual, we calculated social status as normalized David's scores (a dyadic dominance index corrected for chance; de Vries et al., 2006) using the *STEEPNESS* package in R (Leiva & de Vries, 2014). We investigated the relationship between personality and social status within each sex (Table S1). For two of the 24 groups, we did not have enough information on female interactions to calculate female social hierarchies. Because correlations between personality and social status were weak (see Section 3), we included both personality and status as independent effects in subsequent models.

2.2.2 | Aim 1. Precopulatory sexual selection

We examined focal male personality as a predictor of male mating success (number of females mated) and explored whether sex ratio influenced this effect by including interaction terms between male phenotype (personality and social status) and sex ratio in our model (Table S1). We first ran an inclusive GLMM using the *GLMMTMB* package (Brooks et al., 2017), using the data from all three sex ratios combined. Although older males have been demonstrated to gain a lower paternity share than expected, based on their mating performance (McDonald et al., 2017), suggesting age-related declines in sperm numbers and fertilizing efficiency (Cornwallis et al., 2014; Dean et al., 2010), controlling for effects of male age per se did not affect any of the parameters of interest with respect to the effects of male personality on mating performance (Table S2). We tested the overall significance of interaction effects by comparing the full model to a model without a given interaction effect, using a likelihood ratio test (LRT). We then examined the effect of male personality on mating success in each sex ratio, including only the effects that emerged as significant or borderline non-significant (i.e. $0.05 < p < 0.10$) in the inclusive model (Table 1; Table S1). Because there were only eight replicate groups for each sex ratio, we decided to remove fixed and random effects that were of little importance in the inclusive model, when running separate models on each sex ratio.

We next tested the effects of competitors' personality on the relationship between a focal male's personality and his mating success. Because focal boldness was not a significant predictor of male mating success (Table 1), we only focused on exploration. We

TABLE 1 Output of GLMMs examining the predictors of the number of mates obtained for males and females. The reference class for sex ratio is even sex ratio

Predictor	Est. \pm SE	z-value	p
Males (n = 144)			
Exploration	0.128 \pm 0.123	1.045	0.296
Exploration ²	0.031 \pm 0.104	0.301	0.764
Boldness	0.007 \pm 0.089	0.081	0.935
Status	0.263 \pm 0.076	3.443	0.001
Sex Ratio: Male-Biased	-0.753 \pm 0.155	-4.873	<0.001
Sex Ratio: Female-Biased	0.620 \pm 0.146	4.240	<0.001
Exploration \times Sex Ratio: Male-Biased	-0.230 \pm 0.138	-1.670	0.095
Exploration \times Sex Ratio: Female-Biased	-0.156 \pm 0.143	-1.090	0.276
Exploration ² \times Sex Ratio: Male-Biased	0.103 \pm 0.144	0.710	0.478
Exploration ² \times Sex Ratio: Female-Biased	0.594 \pm 0.266	2.237	0.025
Boldness \times Sex Ratio: Male-Biased	-0.058 \pm 0.145	-0.401	0.688
Boldness \times Sex Ratio: Female-Biased	-0.124 \pm 0.166	-0.747	0.455
Status \times Sex Ratio: Male-Biased	-0.088 \pm 0.148	-0.598	0.550
Status \times Sex Ratio: Female-Biased	-0.187 \pm 0.189	-0.990	0.322
Females (n = 138)			
Exploration	-0.039 \pm 0.059	-0.657	0.511
Boldness	0.103 \pm 0.061	1.690	0.091
Normalized David's score	0.044 \pm 0.061	0.717	0.474
Sex Ratio: Male-Biased	0.469 \pm 0.147	3.190	0.001
Sex Ratio: Female-Biased	-0.439 \pm 0.128	-3.424	0.001
Exploration \times Sex Ratio: Male-Biased	-0.097 \pm 0.182	-0.535	0.593
Exploration \times Sex Ratio: Female-Biased	0.047 \pm 0.136	0.348	0.728
Boldness \times Sex Ratio: Male-Biased	0.227 \pm 0.194	1.173	0.241
Boldness \times Sex Ratio: Female-Biased	0.162 \pm 0.140	1.158	0.247
Status \times Sex Ratio: Male-Biased	0.271 \pm 0.177	1.531	0.126
Status \times Sex Ratio: Female-Biased	0.044 \pm 0.139	0.313	0.754

Note: Main effects are reported for the models containing only these predictors. Interaction effects are reported for the models containing both main effects and their interactions. Bold text indicates significant effects.

tested each sex ratio separately, given the influence of sex ratio on the effect of focal personality (Table 1), and we only included fixed effects related to focal phenotype that were significant in the models above (i.e. focal exploration and social status; Table S1).

We also included competitors' exploration and its interaction with focal exploration as fixed effects. We calculated competitors' exploration in two complementary ways: (a) mean competitor exploration and (b) the proportion of competitors with a certain exploration type (e.g. the proportion of fast-exploring competitors) to overcome their respective limitations. Mean competitor personality is contingent on phenotypic distribution (i.e. an intermediate mean value can reflect a group of similarly intermediate phenotypes or a combination of extremely high and extremely low phenotypes). Similarly, measuring the proportion of competitors with a certain personality type requires coarsening a continuous variable into categories. When examining the proportion of fast-exploring competitors, we replaced focal male personality with a binary variable (1 = fast-explorer, 0 = slow-explorer). We classified individuals that had a positive exploration score as fast-explorers and those that had a negative exploration score as slow-explorers. This approach allowed us to test more specifically for frequency-dependent selection. To rule out potential confounding effects due to collinearity between male and female personality across groups, we conducted a Pearson product-moment correlation to test for a relationship between mean female and mean male group personality. We found no evidence of a relationship between mean female and mean male exploration ($r = -0.125$, $p = 0.562$, $n = 24$) or between mean female and mean male boldness across groups ($r = 0.100$, $p = 0.643$, $n = 24$).

2.2.3 | Aim 2. Postcopulatory sexual selection

We first examined whether a female's personality and social status predicted her degree of polyandry (number of males mated) and whether sex ratio modulated this relationship (Table S1). We then estimated the sperm competition intensity (SCI) experienced by a male as the harmonic mean of his partners' mating success:

$$SCI_i = \frac{1}{\frac{1}{M_i} \left(\sum_j \frac{M_j}{k_j} \right)},$$

where M_i is the number of females with whom the i th male mates and k_j is the number of males mated by the j th female (McDonald & Pizzari, 2016; Shuster & Wade, 2003). We examined the effects of male personality and social status on SCI, and assessed whether sex ratio influenced this relationship, using the subset of males that were observed mating with at least one female (Table S1). None of the parameters of interest were affected when we controlled for the effects of male age per se (Table S3). As in Aim 1, we explored the effects of male phenotype on each sex ratio separately, including only the effects that emerged as significant or borderline non-significant in an initial inclusive model (Table 2; Table S1). We also explored whether the relationship between focal male exploration and SCI was influenced by competitors' exploration (Table S1). Given that focal boldness did not predict SCI (Table 2), we did not investigate the effect of competitor boldness composition. Finally, we examined whether male and female

TABLE 2 Output of GLMMs examining the predictors of male sperm competition intensity. The reference class for sex ratio is even sex ratio

Predictor	Est. \pm SE	z-value	p
Males ($n = 108$)			
Exploration	-0.015 ± 0.033	-0.444	0.657
Exploration ²	-0.012 ± 0.029	-0.431	0.667
Boldness	-0.001 ± 0.031	-0.034	0.973
Status	-0.057 ± 0.027	-2.079	0.038
Sex Ratio: Male-Biased	0.371 ± 0.171	2.173	0.030
Sex Ratio: Female-Biased	-0.408 ± 0.164	-2.492	0.013
Exploration \times Sex Ratio: Male-Biased	0.018 ± 0.051	0.351	0.726
Exploration \times Sex Ratio: Female-Biased	-0.023 ± 0.068	-0.334	0.738
Exploration ² \times Sex Ratio: Male-Biased	-0.028 ± 0.057	-0.491	0.623
Exploration ² \times Sex Ratio: Female-Biased	-0.218 ± 0.121	-1.791	0.073
Boldness \times Sex Ratio: Male-Biased	-0.005 ± 0.051	-0.107	0.915
Boldness \times Sex Ratio: Female-Biased	-0.011 ± 0.076	-0.151	0.880
Status \times Sex Ratio: Male-Biased	0.028 ± 0.053	0.531	0.595
Status \times Sex Ratio: Female-Biased	0.073 ± 0.084	0.864	0.388

Note: Main effects are reported for the models containing only these predictors. Interaction effects are reported for the models containing both main effects and their interactions. Bold text indicates significant effects.

focal personality and social status predicted male and female remating rates, respectively, and explored whether sex ratio modulated these effects (Table S1). For these analyses we used only the subset of individuals who mated with at least one partner.

2.2.4 | Aim 3. Assortative or disassortative mating

We examined whether males and females with similar or dissimilar exploration or boldness scores were more likely to mate with one another than expected by chance, given the composition of the group. We calculated the similarity between males and females as the absolute difference between male and female personality scores (e.g. the absolute value of male exploration minus female exploration). Models (Table S1) accounted for every possible pairing of males and females in a group, and we used 1,000 randomizations of mating patterns, holding individual variation in male mating success and female degree of polyandry constant within groups, to generate

1,000 randomized datasets and ran repeated models on these randomized datasets. We then compared empirical slopes with these randomized distributions (Ruxton & Neuhauser, 2013).

2.2.5 | Aim 4. Underpinning mechanisms

We investigated the different behavioural mechanisms underpinning personality-dependent mating patterns. We focused on female preference (measured as solicitation of mating), the relative contribution of male courting (waltzing) and harassment of females, and the physical proximity between individual males and females.

Solicitations

We investigated whether a male's personality and social status predicted the number of solicitations he received, whether a female's personality and social status predicted the number of times she solicited, and whether sex ratio influenced these relationships (Table S1). For the number of solicitations received, we ran an inclusive model that considered data from all sex ratios. When we controlled for the effects of male age per se, none of the parameters of interest were affected (Table S4). We then analysed each sex ratio separately, including only the effects that emerged as significant or borderline non-significant in the inclusive model (Table 4; Table S1). We also tested the effect of competitors' exploration on the relationship between focal exploration and the number of solicitations received within each sex ratio (Table S1). Again, we did not explore the effects of competitor boldness composition, given that a male's boldness did not predict the number of solicitations received (Table 4).

Courtship and harassment

We examined whether a male's personality and social status could predict the proportion of his female-directed behaviours (i.e. intersexual waltzes and harassment events) that were waltzes (i.e. a measurement of the relative contribution of courting; Johnsen et al., 1995; Zuk et al., 1990) and whether sex ratio modulated this relationship (Table S1). Controlling for effects of male age per se had little effect on our parameters of interest, although the interaction between status and female-biased sex ratio became marginally non-significant ($p = 0.052$) when compared to the reference class (Table S5). We then examined the effects of male phenotype on each sex ratio separately, as above (Table 5; Table S1).

Associations

Recent work on the same population indicates that there is a positive correlation between the frequency with which a male associates with a female and the probability that they will mate (McDonald et al., 2019). There is some evidence for similar patterns in other Galliformes (Roth et al., 2021). We calculated the number of times male 'A' was seen associating (≤ 1 body length apart) with female 'B' across scan samples. We also calculated the proportion of successful matings between A and B out of all the successful matings that 'A' gained across all the females in the group. We examined whether

focal male personality and social status, and the proportion of successful matings between a pair, influenced the frequency with which a male associated with a female, and whether males with certain personalities associated disproportionately more with the females with whom they mated more frequently (Table S1). None of the parameters of interest were influenced when we controlled for the effects of male age per se (Table S6).

3 | RESULTS

3.1 | General patterns

Basic patterns of exploration and boldness were not strongly sexually dimorphic in this population (Table S7). Exploration and boldness scores were not inter-correlated across individuals in either sex (Pearson product-moment correlations, males: $r = 0.170$, $p = 0.209$, $n = 56$; females: $r = 0.064$, $p = 0.704$, $n = 38$). Similarly, exploration and boldness were weakly correlated with social status: shyer males were more dominant, and slower exploring females were more dominant (Table S8). Furthermore, when tested against an even sex ratio reference class, shyer females were more dominant in male-biased groups (Table S8); however, the overall interaction between boldness and sex ratio was not significant (LRT, $\chi^2_2 = 4.477$, $p = 0.107$). Group sex ratio influenced patterns of mating behaviour (Table S9) in a way broadly consistent with the expectation that both matings and solicitations will increase as the proportion of females in a group increased (Løvlie & Pizzari, 2007; Pizzari & McDonald, 2019).

3.1.1 | Aim 1. Precopulatory sexual selection

When considering all sex ratio treatments, male mating success was positively correlated with male social status and was lowest in male-biased groups and highest in female-biased groups (Table 1). Importantly, there was some evidence for an interaction between the quadratic term for exploration (henceforth, 'exploration squared') and sex ratio. When compared to an even sex ratio reference class, males at both extremes of the exploration spectrum obtained more mates in female-biased groups (Table 1). There was a non-significant tendency for an overall interaction between sex ratio and exploration squared (LRT, $\chi^2_2 = 5.037$, $p = 0.081$). We explored this further by testing each sex ratio separately and found that males with more extreme exploration scores had higher mating success in female-biased groups (0.452 ± 0.200 ; $z = 2.261$, $p = 0.024$), but not in even sex ratio and male-biased groups (Figure 1; Table S10). Because male social status was not a significant predictor of mating success in female-biased groups, we ran a model for female-biased groups without male social status, which provided a better fit than the model with status ($\Delta\text{AICc} = 2.628$), and obtained similar results for exploration squared (0.542 ± 0.165 ; $z = 3.276$, $p = 0.001$). In addition, we tested whether the relationship between mating success and exploration score in female-biased groups could be predicted by

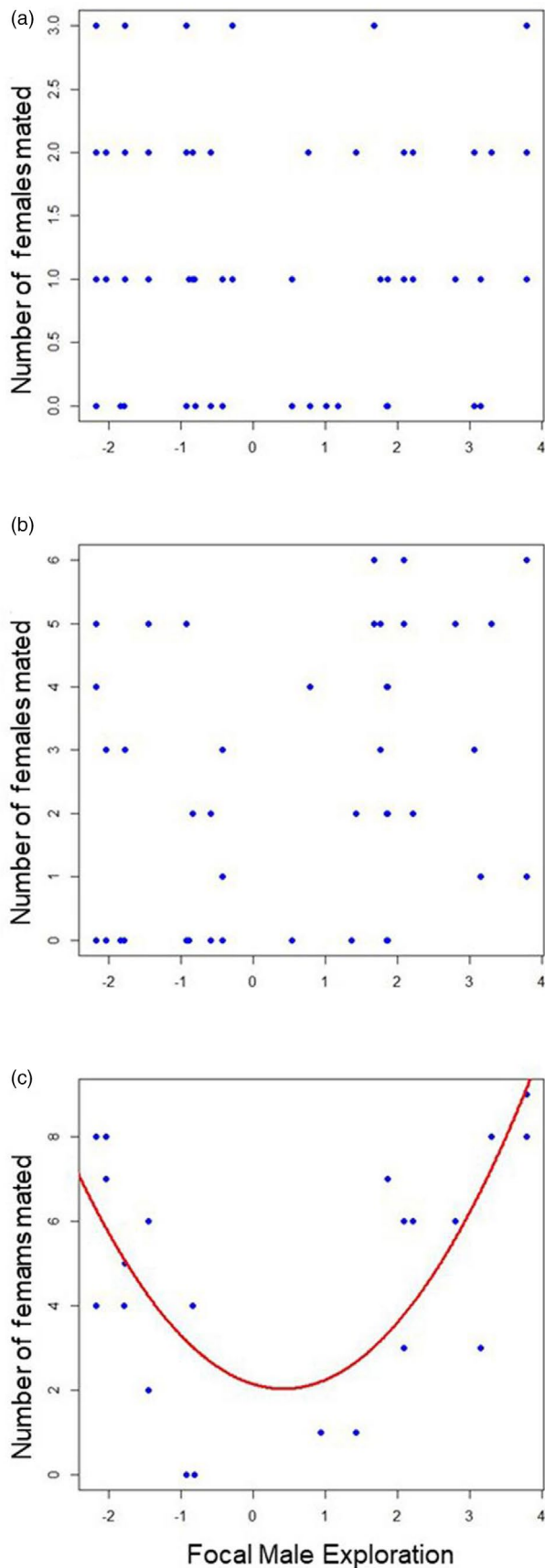


FIGURE 1 The relationship between a focal male's exploration and the number of females he mated with for (a) male-biased, (b) even sex ratio and (c) female-biased groups

social status, using a GLMM with a gamma error structure and log link that included normalized David's score (i.e. social status) as the response, exploration and exploration squared as fixed effects, and individual identity as a random effect. We found that the fastest and slowest exploring males were more likely to be dominant in female-biased groups (0.855 ± 0.356 ; $z = 2.402$, $p = 0.016$; Figure S1), indicating that the effect of exploration squared on mating success may be explained by male social status. Unlike exploration, focal male boldness had no effect on mating success (Table 1).

We then investigated the role of average competitor personality on focal male mating success for each sex ratio treatment separately. In female-biased groups, faster exploring males mated with more females when competitors were, on average, slower exploring and vice versa (Figure 2a; Table S11). Although results were qualitatively similar when competitor exploration composition was defined as the proportion of fast-exploring competitors, this relationship was not significant (Table S11). Because models for female-biased groups were overfit ($n = 24$ with four fixed effects and one random effect), we re-ran models without male social status. When male status was removed, the interaction between focal exploration and competitor exploration was significant (mean exploration: -0.351 ± 0.111 ; $z = -3.167$, $p = 0.002$; proportion of fast-explorers: -1.997 ± 0.750 ; $z = -2.664$, $p = 0.008$). Models without social status provided better fits (lower AICcs) than models with status ($\Delta AICc$: mean exploration = 2.908, proportion of fast-explorers = 2.508). We found no effect of competitors' personality in even and male-biased sex ratios (Table S11). These patterns are consistent with the idea that exploration may be under some negative frequency-dependent selection in female-biased groups, but not in even sex ratio and male-biased groups. We further explored negative frequency-dependent sexual selection on male exploration by running a GLMM with a binomial family and a logit link, using the proportion of matings obtained by fast-exploring males in each of the 24 groups as the response, and the proportion of fast-exploring males in the group, group sex ratio and their interaction as fixed effects. We included female group identity as a random effect. When tested against an even sex ratio reference class, we found a significant negative relationship between the proportion of fast-exploring males in the group and the proportion of matings obtained by fast-exploring males in female-biased groups, suggesting negative frequency-dependent selection (Table S12; Figure 2b). The overall interaction between the proportion of fast-exploring males and sex ratio was significant (LRT, $\chi^2_2 = 26.84$, $p < 0.001$).

3.1.2 | Aim 2. Postcopulatory sexual selection

As expected, average polyandry was highest in male-biased groups and lowest in female-biased groups (Table 1). A female's personality, however, did not predict her degree of polyandry (Table 1).

Similarly, male sperm competition intensity (SCI) was highest in male-biased groups and lowest in female-biased groups (Table 2). A male's SCI was not predicted by his boldness; however, more dominant males experienced lower SCI (Table 2). Furthermore, both faster and slower exploring males showed a tendency to experience lower SCI

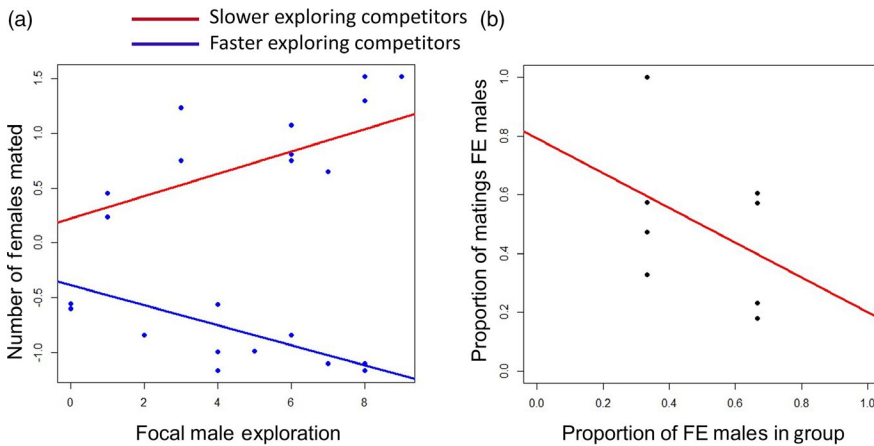


FIGURE 2 (a) In female-biased groups, faster exploring males obtained more mates when competitors were slower exploring, on average, than the focal male, and slower exploring males obtained more mates when competitors were faster exploring, on average, than the focal male. (b) In female-biased groups, the proportion of matings by fast-exploring (FE) males in a group declined as the proportion of FE males in the group increased, suggesting negative frequency-dependent sexual selection

than intermediate males in female-biased groups (Table 2). This quadratic relationship was not significant in the full model, and the interaction between exploration squared and sex ratio was not significant as a whole (LRT, $\chi^2_2 = 3.192$, $p = 0.203$). However, when we examined sex ratios separately, males with more extreme exploration experienced lower SCI in female-biased groups (-0.266 ± 0.114 ; $z = -2.324$, $p = 0.020$), but not even or male-biased sex ratios (Figure 3; Table S13). We also ran a model for female-biased groups that did not include male social status, given that status was not a significant predictor of SCI in female-biased groups, and obtained similar results (-0.349 ± 0.106 ; $z = -3.279$, $p = 0.001$). However, the model with social status provided a better fit ($\Delta\text{AICc} = 44.941$). Competitor exploration did not affect the relationship between a focal male's personality and his SCI (Table S14).

Across all sex ratios, dominant males had higher remating rates with individual females (Table 3). However, neither male personality nor group sex ratio predicted male remating rates (Table 3). Similarly, female personality, social status and group sex ratio did not predict female remating rates (Table 3).

3.1.3 | Aim 3. Assortative or disassortative mating

Males and females of dissimilar boldness scores were more likely to mate with each other (estimate = 0.132, $p_{\text{rand}} = 0.006$; 95% range of simulated estimates = -0.149 to 0.082 ; Figure 4). Randomization tests suggest that this effect, while weak, was stronger than we would expect by chance, controlling for variance in male and female mating success. After performing a Bonferroni correction ($\alpha = 0.05/2$), p -values for disassortative mating based on boldness remained significant. There was no evidence for assortative or disassortative mating with respect to exploration (estimate = -0.095 , $p_{\text{rand}} = 0.342$; 95% range of simulated estimates = -0.129 to 0.024).

3.1.4 | Aim 4. Underpinning mechanisms

Solicitations

As expected, males received the most solicitations in female-biased, and the fewest in male-biased, groups (Table 4). Controlling

for sex ratio, faster exploring and more dominant males received more solicitations (Figure 5a; Table 4). There was no evidence that mean competitor exploration influenced the relationship between male exploration and solicitations received in any sex ratio treatment (Table S15). Finally, female personality and social status had no effect on the number of solicitations given by a female (Table 4).

Courtship and harassment

Subdominant males dedicated proportionally fewer waltzes to females than more dominant males, particularly in female-biased groups (Table 5). Controlling for social status and sex ratio treatment, however, males with more extreme exploration scores courted females proportionally less, compared to males with intermediate exploration scores (Figure 5b; Table 5). There was no interaction between exploration squared and sex ratio, and exploration squared was not a significant predictor of the proportion of waltzes when each sex ratio was analysed separately (Table 5; Table S16). Furthermore, we found that bolder males courted females proportionally less in male-biased than in even sex ratio groups (Table 5). While the interaction between male boldness and sex ratio was significant as a whole (LRT, $\chi^2_2 = 8.420$, $p = 0.015$), male boldness did not predict the proportional investment in courting in any of the sex ratios analysed separately (Table S16). We also ran a model for male-biased groups that did not include exploration or exploration squared and obtained similar results for boldness and social status (boldness: -0.179 ± 0.122 , $z = -1.466$, $p = 0.142$; social status: 0.223 ± 0.085 , $z = 2.617$, $p = 0.009$). This simpler model provided a slightly better fit than the model with exploration and exploration squared ($\Delta\text{AICc} = 1.100$).

Associations

Controlling for sex ratio, males associated more with the females with whom they mated more frequently, and faster exploring and dominant males associated more with females, than did slower exploring or subdominant males, regardless of how often they mated with these females (Figure 5c; Table 5). The highest number of associations was between faster exploring males and the females with whom they mated more frequently (Table 5).

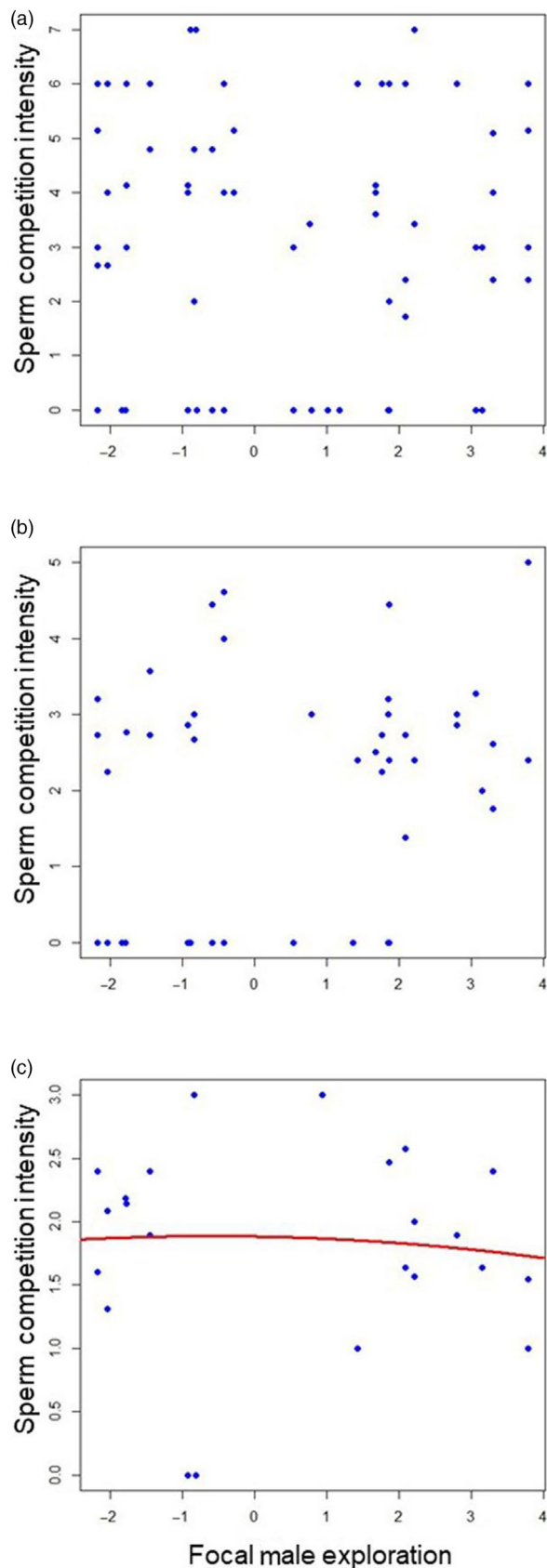


FIGURE 3 The relationship between the focal male's exploration and the sperm competition intensity he experienced for (a) male-biased groups, (b) even sex ratio groups and (c) female-biased groups

TABLE 3 Output of GLMMs examining the predictors of remating rates for males and females. The reference class for sex ratio is even sex ratio

Predictor	Est. \pm SE	z-value	p
Males (n = 108)			
Exploration	0.148 \pm 0.097	1.527	0.127
Exploration ²	0.094 \pm 0.057	1.657	0.098
Boldness	0.003 \pm 0.072	0.036	0.971
Status	0.200 \pm 0.050	3.991	<0.001
Sex Ratio: Male-Biased	-0.111 \pm 0.189	-0.587	0.557
Sex Ratio: Female-Biased	0.208 \pm 0.194	1.070	0.285
Exploration \times Sex Ratio: Male-Biased	0.055 \pm 0.080	0.688	0.492
Exploration \times Sex Ratio: Female-Biased	-0.083 \pm 0.107	-0.771	0.441
Exploration ² \times Sex Ratio: Male-Biased	0.040 \pm 0.089	0.442	0.659
Exploration ² \times Sex Ratio: Female-Biased	0.164 \pm 0.197	0.832	0.406
Boldness \times Sex Ratio: Male-Biased	-0.008 \pm 0.083	-0.090	0.928
Boldness \times Sex Ratio: Female-Biased	-0.071 \pm 0.125	-0.565	0.572
Status \times Sex Ratio: Male-Biased	0.112 \pm 0.085	1.319	0.187
Status \times Sex Ratio: Female-Biased	0.080 \pm 0.130	0.611	0.541
Females (n = 131)			
Exploration	0.081 \pm 0.084	0.968	0.333
Boldness	0.058 \pm 0.067	0.869	0.385
Normalized David's score	0.052 \pm 0.051	1.024	0.306
Sex Ratio: Male-Biased	0.227 \pm 0.190	1.194	0.233
Sex Ratio: Female-Biased	0.170 \pm 0.166	1.022	0.307
Exploration \times Sex Ratio: Male-Biased	-0.091 \pm 0.164	-0.554	0.580
Exploration \times Sex Ratio: Female-Biased	-0.043 \pm 0.086	-0.506	0.613
Boldness \times Sex Ratio: Male-Biased	0.003 \pm 0.164	0.021	0.984
Boldness \times Sex Ratio: Female-Biased	-0.013 \pm 0.087	-0.154	0.878
Status \times Sex Ratio: Male-Biased	0.048 \pm 0.143	0.334	0.738
Status \times Sex Ratio: Female-Biased	-0.046 \pm 0.096	-0.477	0.634

Note: Main effects are reported for the models containing only these predictors. Interaction effects are reported for the models containing both main effects and their interactions.

4 | DISCUSSION

While sexual selection has been suggested as a fundamental process modulating variation of personality in populations (Schuett

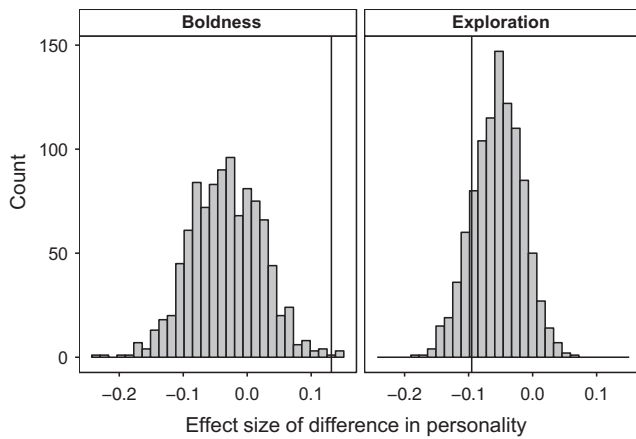


FIGURE 4 Individuals mated disassortatively with respect to boldness, but randomly with respect to exploration. Grey bars represent randomized distributions of effect sizes, and the vertical lines represent the empirical slopes

et al., 2010), little is known about the way in which sexual selection targets personality. Using replicate groups of red junglefowl, we experimentally manipulated group sex ratio and personality composition to examine the role of personality in precopulatory sexual selection and some forms of postcopulatory sexual selection, polyandry, assortative mating and the behavioural mechanisms governing these patterns. In addition to examining the effects of focal individuals' personality on mating performance, we also explored group-level effects by analysing the influence of competitors' personality.

4.1 | Correlations between different measures of personality

We found that a tendency to explore a novel environment (exploration) did not correlate with a tendency to investigate a novel object (boldness) in our study population. Similar results have been found in other fowl populations (Favati et al., 2016, 2018), as well as in mountain chickadees *Poecile gambeli* (Fox et al., 2009). In contrast, a correlation between exploration and boldness has been shown in a number of species, including great tits (Verbeek et al., 1994), bluegill sunfish *Lepomis macrochirus* (Wilson & Godin, 2009) and zebra finches *Taeniopygia guttata* (David et al., 2011). It is possible that ecological conditions may affect the evolution of correlations between behavioural traits (Bell & Sih, 2007; Dingemanse et al., 2007). For example, in different populations of three-spined sticklebacks *Gasterosteus aculeatus*, correlations between activity, aggressiveness and exploration behaviour vary due to differences in the size and predation pressure of home ponds (Dingemanse et al., 2007). Although among-individual correlations between different behavioural traits may influence the net selective forces operating on each trait (Dochtermann & Dingemanse, 2013; Lande & Arnold, 1983), a lack of correlation between behavioural traits suggests that sexual selection may act independently on exploration and boldness in our study population.

TABLE 4 Output of GLMMs examining the predictors of the number of solicitations received by males and the number of solicitations given by females. The reference class for sex ratio is even sex ratio

Predictor	Est. \pm SE	z-value	p
Males (n = 144)			
Exploration	0.541 \pm 0.247	2.196	0.028
Exploration ²	0.165 \pm 0.151	1.097	0.273
Boldness	0.030 \pm 0.172	0.174	0.862
Status	0.579 \pm 0.154	3.762	<0.001
Sex Ratio: Male-Biased	-0.962 \pm 0.330	-2.917	0.004
Sex Ratio: Female-Biased	1.941 \pm 0.269	7.208	<0.001
Exploration \times Sex Ratio: Male-Biased	-0.516 \pm 0.595	-0.867	0.386
Exploration \times Sex Ratio: Female-Biased	-0.877 \pm 0.521	-1.685	0.092
Exploration ² \times Sex Ratio: Male-Biased	0.493 \pm 0.410	1.204	0.229
Exploration ² \times Sex Ratio: Female-Biased	0.497 \pm 0.513	0.970	0.332
Boldness \times Sex Ratio: Male-Biased	-0.345 \pm 0.406	-0.850	0.396
Boldness \times Sex Ratio: Female-Biased	0.029 \pm 0.300	0.098	0.922
Status \times Sex Ratio: Male-Biased	-0.616 \pm 0.391	-1.577	0.115
Status \times Sex Ratio: Female-Biased	0.007 \pm 0.343	0.020	0.984
Females (n = 138)			
Exploration	0.082 \pm 0.136	0.601	0.548
Boldness	0.029 \pm 0.122	0.235	0.814
Normalized David's score	-0.184 \pm 0.126	-1.461	0.144
Sex Ratio: Male-Biased	0.387 \pm 0.358	1.082	0.279
Sex Ratio: Female-Biased	0.784 \pm 0.243	3.223	0.001
Exploration \times Sex Ratio: Male-Biased	-0.784 \pm 0.505	-1.552	0.121
Exploration \times Sex Ratio: Female-Biased	0.032 \pm 0.260	0.124	0.901
Boldness \times Sex Ratio: Male-Biased	-0.131 \pm 0.485	-0.271	0.787
Boldness \times Sex Ratio: Female-Biased	-0.136 \pm 0.295	-0.462	0.644
Status \times Sex Ratio: Male-Biased	0.075 \pm 0.454	0.165	0.869
Status \times Sex Ratio: Female-Biased	0.231 \pm 0.271	0.853	0.394

Note: Main effects are reported for the models containing only these predictors. Interaction effects are reported for the models containing both main effects and their interactions. Bold text indicates significant effects.

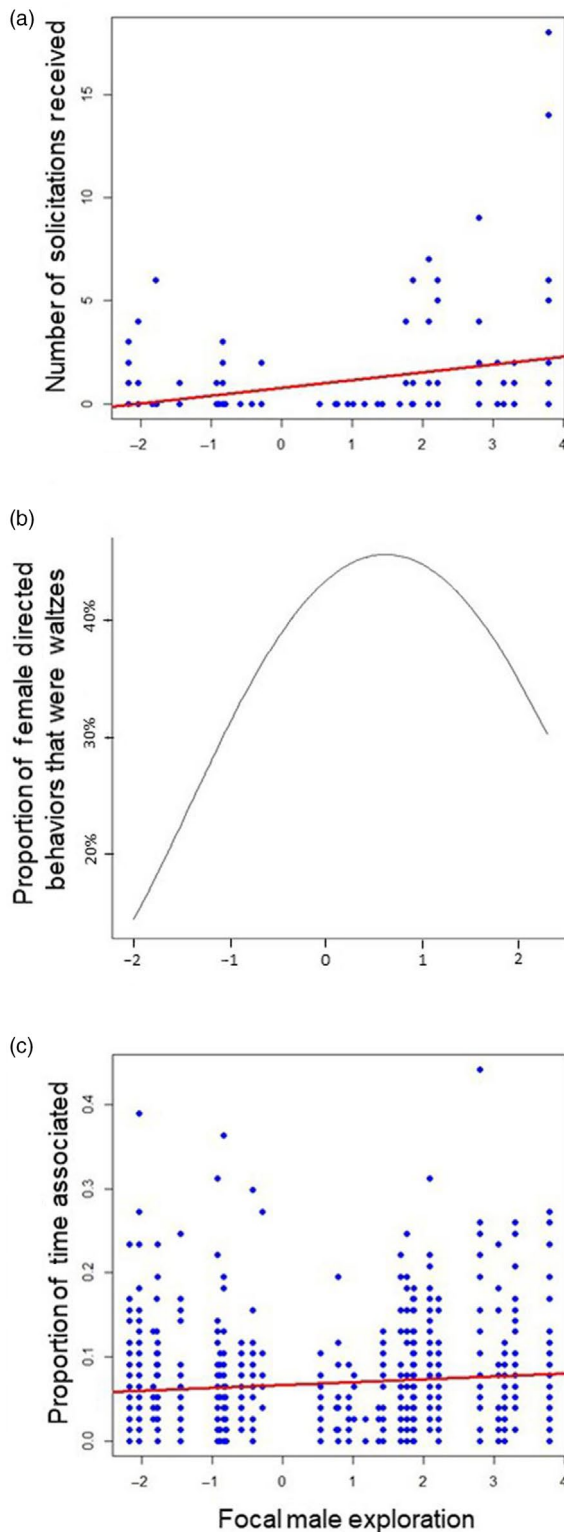


FIGURE 5 (a) Faster exploring males received more solicitations than slower exploring males. (b) Of the female-directed behaviours recorded (waltzing plus harassment), extreme-exploring males had lower proportions of waltzes than intermediate-exploring males. The plotted curve in this graph was based on predicted values, rather than raw data, as the random effects included in this model had large effects on the relationship between male exploration and the proportion of waltzes observed. (c) Faster exploring males associated slightly more with females than slower exploring males

4.2 | Personality as a predictor of social status

We found some evidence suggesting weak linear relationships between personality and social status in both sexes. Slower exploring females and shyer individuals of both sexes were more dominant, although for females, correlations between boldness and social status were only observed in male-biased groups. Previous work in domestic fowl has demonstrated that faster exploring males are more likely to be dominant; however, this relationship was only observed in dyadic contests (Favati, Leimar, & Løvlie, 2014; Favati Løvlie & Leimar, 2017). In larger groups, neither boldness nor exploration was found to predict social rank (Favati, Leimar, & Løvlie, 2014; Favati et al., 2017). Across other species, the relationship between personality and social status is inconsistent, with faster explorers dominating slower explorers in some studies (Cole & Quinn, 2011; David et al., 2011; Verbeek et al., 1996), and vice versa in others (Fox et al., 2009). Similarly, bolder individuals dominate shyer individuals in some studies (Colléter & Brown, 2011; Dahlbom et al., 2011; Sundström et al., 2004), and vice versa in others (Taylor & Lattanzio, 2016). Moreover, relationships between personality and social status may be context-dependent (Dingemanse & de Goede, 2004). For example, in great tits, faster exploring territorial males have been shown to be dominant over slower exploring territorial males, while slower exploring non-territorial juvenile males have been shown to have higher status than their faster exploring counterparts (Dingemanse & de Goede, 2004). Although personality differences may arise as a result of dominance relationships (Arakawa, 2006; Barnard & Luo, 2002; Favati, Leimar, Radesäter, et al., 2014), personality may also drive patterns of social status (Fox et al., 2009; Schjolden et al., 2005). Individuals with dissimilar personality types may respond to stress differently, fostering discrepancies in status between individuals (Fox et al., 2009). For example, in domestic fowl, Japanese quail *Coturnix japonica*, and great tits, individuals that respond more fearfully in novel arena tests often respond to stress by mounting a greater corticosterone response than less fearful individuals (reviewed in Cockrem, 2007). It is also possible that the repeatable behaviours examined in our study correlate with a latent trait we did not examine, such as aggression, which is strongly related to social status in fowl (Favati, Leimar, & Løvlie, 2014; Favati Løvlie, & Leimar, 2017; Pizzari & McDonald, 2019) and other species (e.g. Armitage & van Vuren, 2003; Bolhuis et al., 2005; Pottinger & Carrick, 2001; Verbeek et al., 1996). Favati et al. (2017) demonstrated that boldness, but not exploration, correlates positively with aggression in male domestic fowl. Finally, relationships between personality and social status may exist if personality influences responses to social defeat (Verbeek et al., 1999). For example, although faster exploring great tits have been shown to be more aggressive and more likely to win dyadic contests, slower exploring individuals have been shown to recover more quickly from social defeat, allowing them to achieve higher social status in group settings (Verbeek et al., 1996, 1999). In male domestic fowl, however, winner-loser effects may not predict social rank (Favati et al., 2017); thus, any influence of personality on social defeat is unlikely to have long-term repercussions for social status in male domestic fowl, and potentially red junglefowl. The evidence of possible relationships between male personality and social status in red junglefowl detected

Predictor	Est. \pm SE	z-value	p
Waltzes:Harassment (n = 144)			
Exploration	0.056 \pm 0.104	0.541	0.589
Exploration ²	-0.134 \pm 0.044	-3.026	0.002
Boldness	0.059 \pm 0.090	0.659	0.510
Status	0.181 \pm 0.041	4.436	<0.001
Sex Ratio: Male-Biased	-0.235 \pm 0.325	-0.723	0.470
Sex Ratio: Female-Biased	0.354 \pm 0.349	1.015	0.310
Exploration \times Sex Ratio: Male-Biased	-0.033 \pm 0.054	-0.601	0.548
Exploration \times Sex Ratio: Female-Biased	-0.050 \pm 0.084	-0.601	0.548
Exploration ² \times Sex Ratio: Male-Biased	0.053 \pm 0.060	0.878	0.380
Exploration ² \times Sex Ratio: Female-Biased	0.203 \pm 0.135	1.497	0.134
Boldness \times Sex Ratio: Male-Biased	-0.195 \pm 0.068	-2.881	0.004
Boldness \times Sex Ratio: Female-Biased	-0.044 \pm 0.087	-0.511	0.610
Status \times Sex Ratio: Male-Biased	-0.055 \pm 0.066	-0.837	0.403
Status \times Sex Ratio: Female-Biased	0.167 \pm 0.085	1.969	0.049
Associations (n = 720)			
Proportion of Successful Matings	0.703 \pm 0.069	10.158	<0.001
Exploration	0.147 \pm 0.073	2.016	0.044
Exploration ²	0.004 \pm 0.041	0.095	0.925
Boldness	-0.078 \pm 0.055	-1.405	0.160
Status	0.243 \pm 0.030	8.108	<0.001
Sex Ratio: Male-Biased	0.165 \pm 0.128	1.290	0.197
Sex Ratio: Female-Biased	-0.405 \pm 0.133	-3.041	0.002
Exploration \times Proportion of Successful Matings	0.165 \pm 0.068	2.424	0.015
Exploration ² \times Proportion of Successful Matings	0.039 \pm 0.083	0.472	0.637
Boldness \times Proportion of Successful Matings	0.008 \pm 0.069	0.119	0.905
Status \times Proportion of Successful Matings	-0.003 \pm 0.074	-0.035	0.972

Note: Main effects are reported for the models containing only these predictors. Interaction effects are reported for the models containing both main effects and their interactions. Bold text indicates significant effects.

in our study is especially important given that, consistent with previous studies (Collias & Collias, 1996; Kim & Zuk, 2000; Lill, 1966; Pizzari & McDonald, 2019; Thornhill, 1988), we found that male social status often predicted male mating performance.

4.3 | Personality and social status as predictors of reproductive performance and strategy

There was little evidence for male boldness playing an important role in sexual selection, although it should be noted that

TABLE 5 Output of GLMMs examining the predictors of the proportion of waltzes over the total number of female-directed behaviours (waltzes plus harassments) displayed by a male and the number of times a male was seen associating with a female (out of 77 possible scan samples). The reference class for sex ratio is even sex ratio

male boldness was only weakly repeatable, and not significantly so, which may represent a type II statistical error given the low sample size (Dingemanse & Dochtermann, 2013). Male exploration, on the other hand, appeared to be important, especially in female-biased groups. In this sex ratio, males at both extremes of the exploration spectrum mated with more females and experienced lower sperm competition intensity (SCI) than intermediate males. Our results are consistent with past work, showing that males which obtain more mates also suffer lower SCI (McDonald et al., 2017). Moreover, our results support previous studies suggesting that a male's personality is tied to his mating performance.

For example, in young bighorn sheep *Ovis canadensis*, less docile males were shown to have higher reproductive success than more docile males; however, at an older age, more docile males gained a reproductive advantage (Réale et al., 2009). Similarly, active-aggressive males were shown to have higher mating success than less active-aggressive or hyper-aggressive males in water striders (Sih et al., 2014). Overall, our results suggest that, in female-biased groups, disruptive pre- and postcopulatory sexual selection may promote extremely fast- and slow-exploring males, at the expense of males of intermediate phenotype. Nevertheless, it is important to point out that we did not directly test for variation in paternity share in relation to personality, and future work should explore this further.

Mating advantages for extreme-exploring males may arise as a result of inherent differences between extreme and intermediate-exploring male mating strategies and/or social status. For example, we found that, of the total number of female-directed behaviours (waltzing and harassment), males at both extremes of the exploration spectrum expressed lower proportions of waltzes than intermediate-exploring males. Waltzing represents a form of male courtship and may be less costly to females than harassment (Johnsen et al., 1995; Zuk et al., 1990), and our results suggest that, in our population, extreme-exploring males might pursue different reproductive strategies from intermediate-exploring males. Furthermore, we found that in female-biased groups, the fastest and slowest exploring males were more likely to achieve higher social status than intermediate-exploring males, suggesting that, in these groups, males with extreme exploration scores may attain more mates through status. The fact that male social status did not predict mating success in female-biased groups could, therefore, be due to a masking effect of male exploration. Alternatively, these results could reflect female preference, as female-biased groups may be characterized by limited competition among males and more active female mating strategies (Løvlie & Pizzari, 2007). These results, however, must be interpreted with caution due to the limited sample size, which often resulted in overfit models when we examined female-biased sex ratios in isolation. We sought to address this by removing less important fixed and random effects from the models, but future studies should focus on investigating the role of male exploration in female-biased groups in more depth.

Extreme male exploration types may acquire mating advantages via alternative channels. For example, slower explorers may benefit by staying in areas with higher female density, leading to increased opportunities for mating. In contrast, faster explorers may cover a greater spatial area and encounter females more frequently. Faster explorers may also be more likely to follow females as they move, leading to increased access to individual partners. This is supported by the fact that, in addition to finding that the greatest number of associations occurred between faster exploring males and the females with whom they mated more frequently, faster exploring males were also generally more likely to associate with females than slower exploring males. Previous work on this population suggests that pairs that associate more frequently are more likely to mate (McDonald

et al., 2019). Moreover, females may prefer faster exploring males if these traits confer a direct or genetic benefit to females, or if exploration is correlated with another potentially preferred trait such as learning speed (e.g. Zidar et al., 2018). For example, faster exploring males may acquire more or higher quality food for courtship feeding of females, as they cover more ground while foraging. Indeed, we found that females solicited faster exploring males more than their slower exploring counterparts.

A male's mating performance also appeared to be influenced by the exploration behaviour of his competitors. In female-biased groups, but not in even or male-biased sex ratios, faster exploring males attained more mates when competitors were slower exploring on average and vice versa. In water striders, a male's mating performance was reduced when a hyper-aggressive male was present in the group (Sih et al., 2014). However, in contrast to our results, in water striders, the effects of group personality composition on mating performance were not found to depend on the focal individual's phenotype (Sih et al., 2014). We also found that in female-biased groups, fast-exploring males mated proportionally more when there was a lower proportion of fast-exploring males in the group. These results suggest that male exploration may be under negative frequency-dependent sexual selection. This may contribute to the maintenance of interindividual variation in exploration, in that, when the proportion of fast-explorers increases, slow-explorers gain a fitness advantage and vice versa. Such fitness advantages may arise due to the 'rare male effect' if rare type males experience decreased male-male competition, for instance, in situations where intraphenotypic competition for mates outweighs interphenotypic competition, or if females prefer rare type males (reviewed in Knopien, 1985). The results of our study suggest that individual variation in mating performance may be related to the frequency of personality types in a group. Moreover, the fact that social conditions favoured rarer, more extreme exploration phenotypes may help explain the quadratic relationship between focal exploration and male mating success. It is important to note, however, that when trait distributions are continuous, rather than bimodal, as was the case for the behavioural traits examined in our study, a challenge to testing for negative frequency dependence is that phenotypes are categorized by binning variables based on artificial cut-offs. Nevertheless, analyses based on mean group personality were largely qualitatively consistent with models using proportions of personality categories.

In addition to finding that faster exploring males received a higher number of solicitations from females, females also solicited more to dominant males, which supports past work (Pizzari & McDonald, 2019). It should, however, be noted that we did not test for potential effects of personality on cryptic female choice (Firman et al., 2017), and future work should explore this possibility. We found little evidence that male boldness is targeted by sexual selection. However, the patterns of non-random disassortative mating seen in this study with respect to boldness are consistent with work in other species showing that mating is more common between individuals with dissimilar personality types (Dingemanse et al., 2004; but see Harris & Siefferman, 2014; Kralj-Fišer et al., 2013), and suggest that

variation in boldness might contribute to determine the compatibility or affinity of different mating combinations. A recent criticism of past work examining assortative mating for labile traits, such as personality, is that apparent non-random assortment may arise from processes unrelated to individuals preferentially selecting partners that are phenotypically similar or dissimilar to themselves (Class et al., 2017; Dingemanse et al., 2020; Munson et al., 2020). Such processes include shared responses to the environment, convergence of phenotypes between members of a pair after mating, correlated measurement error and scale of choice effects. For example, a positive correlation may arise between the phenotypes of mated individuals because partners show similar responses to shared environmental conditions. However, we avoided such biases by conducting personality assays prior to group formation and after individuals experienced different environmental conditions than their mates. If boldness in red junglefowl is heritable, the observed disassortative mating may initially reduce phenotypic variation by producing offspring of intermediate phenotype (e.g. in the first generation) and could contribute to genetic variation in this trait over time.

Several previous studies have demonstrated links between male personality and male mating strategies (Patrick et al., 2011; Reaney & Backwell, 2007) and/or female preferences (Dziewieczynski et al., 2013; Godin & Dugatkin, 1996; Reaney & Backwell, 2007; Schuett et al., 2011; Teyssier et al., 2014). For example, in one population of socially monogamous great tits, faster exploring males invested more in extra-pair paternity, while slower exploring males invested more in within-pair paternity, despite there being no differences between phenotypes in total paternity (i.e. within-pair plus extra-pair paternity; Patrick et al., 2011; but see Abbey-Lee et al., 2018; Araya-Ajoy et al., 2016; Roth et al., 2019). Similarly, bolder male fiddler crabs have been shown to court females more than shyer males, winning female preference and obtaining more mates (Reaney & Backwell, 2007). Females also prefer bolder males in Trinidadian guppies *Poecilia reticulata* (Godin & Dugatkin, 1996), and moderate and faster exploring female zebra finches have been shown to prefer exploratory over unexploratory males (slower exploring females showed no preference; Schuett et al., 2011).

Overall, we present evidence suggesting that male personality may play important but complex roles in precopulatory and some forms of postcopulatory sexual selection in a captive population of red junglefowl. Although some past research has demonstrated links between a focal individual's personality and its reproductive performance in some species, most of this work has been conducted on a single sex ratio treatment, and little is known about the way the personality of competitors or potential mates might influence an individual's reproductive performance or the underlying mechanisms driving interindividual variation in reproductive success. While some caution should be applied when interpreting our results, given that we did not explicitly control for multiple comparisons and given that significance levels were occasionally moderate, patterns were consistent across numerous analyses. Sexual selection on male personality appears particularly pronounced in female-biased groups where males with extremely high and low exploration have an advantage. We show

that the personality composition of a group modulates the way sexual selection affects the personality of focal males (e.g. faster exploring males are particularly favoured when their competitors are, on average, slower exploring), suggesting negative frequency-dependent selection. To the best of our knowledge, our study provides some of the first empirical support of negative frequency-dependent sexual selection acting on personality. We also show disassortative mating based on boldness. The combination of disruptive selection, negative frequency dependence and disassortative mating may contribute to the maintenance of genetic variation potentially underpinning these repeatable behaviours in this species.

ACKNOWLEDGEMENTS

We gratefully acknowledge Louisa Gould, Rory Meryon, Helen Nuttall, Chloe Randall and James Worthington for their assistance in data collection. We thank David Wilson and Lucy Larkman for animal husbandry. We appreciate comments from Jen Perry, Wiebke Schuett and an anonymous Associate Editor and two anonymous reviewers at the *Journal of Animal Ecology*, which improved the manuscript. A.M.R. was supported by scholarships from St. Catherine's College, University of Oxford.








AUTHORS' CONTRIBUTIONS

A.M.R., T.P., N.J.D. and H.L. were involved in the initial project conceptualization and design; A.M.R. constructed the first draft of the manuscript and revised further drafts according to input from all coauthors; A.M.R. conducted the statistical analyses, with exception to the analyses for assortative and disassortative mating, which were performed by G.C.M. G.C.M., N.J.D. and S.N. provided critical statistical guidance; S.N. wrote the code contained in Appendix S2, used to test repeatability in exploration and boldness; N.J.D. and H.L. provided valuable guidance regarding animal personality; A.M.R. collected the data with assistance from D.R. All authors approved the final version of this manuscript for publication.

DATA AVAILABILITY STATEMENT

Data are publicly available on Figshare <https://doi.org/10.6084/m9.figshare.13951640.v1> (Roth et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Roth AM, Dingemanse NJ, Nakagawa S, et al. Sexual selection and personality: Individual and group-level effects on mating behaviour in red junglefowl. *J Anim Ecol*. 2021;90:1288–1306. <https://doi.org/10.1111/1365-2656.13454>