Exploring the Intersection between Animal Personality and Sociality

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ABSTRACT

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A topic of growing interest in behavioral ecology centers around the causes and consequences of animal personality - defined as consistent interindividual differences in behavior. Although much work has focused on examining the relationships between an individual's personality and its fitness, limited knowledge exists regarding how variation in personality is maintained or how the personalities of competitors and actual or potential mates may play into this. Furthermore, few studies have examined how other aspects of an individual's social environment (e.g. competition levels) might influence relationships between focal personality and fitness, or how the combined personalities of individuals in a group might affect emergent group properties. A main objective of this thesis was to explore how the relationship between focal personality and reproductive performance is modulated by the social environment. In doing so, I aimed to elucidate potential mechanisms that help maintain variation in personality within populations. I progressed from examining the individual level consequences of personality to investigating the effects of group personality composition on emergent group dynamics which, while not examined here, could promote differential fitness between groups.

My thesis demonstrates the potential for an individual's social environment to interact with its personality to affect reproductive performance. In great tits, I found evidence to suggest that the species composition, but not the conspecific personality composition, of birds breeding in the vicinity of a focal bird, modulated the relationship between focal personality and reproductive performance. Males with different personality types became increasingly similar in the proportion of their clutch fledged with increasing ratios of blue tit to great tit neighbors, suggesting that relaxing the amount of intra- versus interspecific competition led males to converge in reproductive performance. It appears that heterogeneity in an individual's social environment might influence selection on exploration behavior, but that it is not sufficient in itself to maintain interindividual variation in this behavioral trait. In female-biased red junglefowl groups, I found that slower-exploring males mated with more females when their competitors were faster-exploring, on average, and vice versa. Furthermore, in female-biased groups, the proportion of matings attained by faster-exploring males rose with increasing proportions of slower-exploring males in a group, suggesting negative frequency dependent sexual selection may help maintain interindividual variation in exploration. Lastly, I found that group personality composition in red junglefowl may affect the mean number of aggressive, affiliative, and sexual harassment interactions occurring within the group, as well as the social network structure of these interactions, particularly network density. Understanding the factors that influence network structure are important for our knowledge of processes like disease transmission and information flow, and future work should examine how such emergent group properties might impact group level fitness.

In conclusion, this thesis improves our understanding of the consequences and maintenance of animal personality. It expands upon past work looking at the reproductive consequences of a focal individual's personality to examine how the social environment may work to shape the relationships between focal personality and reproductive performance. Future work should examine the broader ecological and evolutionary consequences of my results and how individual and group level outcomes might influence population and community dynamics.

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Author Contributions

Main Contributors

Allison M. Roth had independent intellectual input into all aspects of the thesis, designed red junglefowl experiments and personality assays, and collected the personality, reproductive, and social network data used for both red junglefowl chapters (Chapters 3 and 5). Also analyzed data for all data chapters, wrote drafts, and incorporated coauthor comments to produce the finished chapters.

Ben C. Sheldon (supervisor and co-author of Chapters 2 and 4) provided intellectual input, guidance on data analysis, and offered feedback on drafts of Chapters 2 and 4.

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Ella F. Cole (co-supervisor and co-author of Chapters 2 and 4) provided intellectual input, guidance on data analysis, and offered feedback on drafts of Chapters 2 and 4.

Josh A. Firth (co-author of Chapters 2 and 4) provided intellectual input, guidance on data analysis, and offered feedback on drafts of Chapters 2 and 4. Also constructed Voronoi polygons used for Chapters 2 and 4 and provided guidance on the social network analyses used in Chapter 5.

Additional Contributors

Shinichi Nakagawa (co-author of Chapter 3) designed the methods and wrote the code used to test for repeatability in continuous, nonnormal red junglefowl personality data and provided feedback on drafts of Chapter 3.

Grant C. McDonald (co-author of Chapter 3) provided guidance on data analysis for Chapter 3, conducted the assortative mating analyses for Chapter 3, and provided feedback on drafts of this chapter.

Niels Dingemanse (co-author of Chapter 3) provided guidance in the design of the red junglefowl personality assays and provided feedback on drafts of Chapter 3.

Hanne Løvlie (co-author of Chapter 3) provided guidance in the design of the red junglefowl personality assays and provided feedback on drafts of Chapter 3.

Samantha C. Patrick (co-author of Chapter 2) collected paternity data used for Chapter 2 and provided feedback on drafts of this chapter.

Diana Robledo-Ruiz (co-author of Chapter 3) collected a small portion of the data used for the red junglefowl chapters (Chapters 3 and 5) and provided feedback on drafts of Chapter 3.

Contents

Chapter 1

General Introduction

GENERAL INTRODUCTION

Scientific interest in, and understanding of, interindividual phenotypic variation has undergone many stages. In 1859, Darwin first published his book On the Origin of Species, and for many decades following this pivotal work, scientists focused on how interindividual differences could promote speciation (Wilson 1998). As evolutionary biology and ecology progressed, interest in the fitness consequences of between-individual phenotypic differences within species and populations arose, yet at first, researchers favored examining morphological and physiological traits over interindividual behavioral variation (Reznick & Endler 1982; Price et al. 1984; Whitfield 1987; Wilson 1998). This slowly started to shift upon the discovery of discrete alternative mating tactics (e.g. Gross 1984; 1991; Shuster & Wade 1991; Sinervo & Lively 1996), yet even then, it would be around a decade before scientists started to recognize that individuals are also often limited in their range of expression of continuous behavioral traits. Nevertheless, in the past 25 years, or so, the concept of "animal personality" has risen to the forefront of ecological and evolutionary research (Verbeek et al. 1994; 1996; Dall et al. 2004; Sih et al. 2004a; Dingemanse & Réale; 2005; Bell et al. 2009).

Animal personality may be defined as interindividual differences in behavior that are consistent within individuals, across different situations or contexts (Dall et al. 2004; Sih et al. 2004a; Dingemanse & Réale; 2005; Bell et al. 2009). Personality has been demonstrated in a wide range of taxa including birds, mammals, lizards, amphibians, fish, molluscs, and arthropods (Gosling 2001; Dingemanse et al. 2002; Quinn et al. 2009; Sih et al. 2004a; van Oers et al. 2004a,b). Importantly, the realization that personality constrains behavioral plasticity can drastically alter the way we understand the ecology and evolution of behavior, enhancing our understanding of speciation, population dynamics, and interindividual differences in survival and reproduction. Over the last couple of decades, two central questions have developed in personality research concerning 1) why intraindividual consistency in behavior exists (Box 1) and 2) how interindividual variation in personality is maintained within populations across time. This thesis will explore the latter.

Box 1: Why does intraindividual consistency in behavior exist?

A central question that arises in personality research concerns the evolution and maintenance of intraindividual consistency in behavior (Dall et al. 2004; Sih et al. 2004b; Wolf et al. 2008; McNamara et al. 2009; Schuett et al. 2010; Wolf & Weissing; 2010). From an evolutionary standpoint, it may seem maladaptive to impose constraints on behavior, as flexibility should provide a selective advantage. However, some studies suggest that behavioral consistency reduces a number of costs that may be associated with behavioral flexibility (Tufto 2000; Sih et al. 2004; Dall et al. 2004). In an ever-changing environment, formulating an adaptive response to current environmental conditions may increase success in the local environment but decrease one's certainty regarding alternative environmental states, as information about such states wanes when they are not being faced (Dall & Cuthill 1997; Dall et al. 2004). Thus, individuals may have a higher chance of responding inappropriately, or take longer to respond appropriately, when faced with alternative conditions, and the costs of such errors may select for developmental canalization (Tufto 2000; Dall et al. 2004; Sih et al. 2004b).

Furthermore, there may be benefits to behavioral predictability (Dall et al. 2004; McNamara et al. 2009; Schuett et al. 2010). For example, if an individual is predictable in its levels of aggression, and eavesdropping is present, conspecifics may be able to avoid more aggressive individuals, and thus circumvent costly fights. This is not only beneficial for the eavesdropping individuals, but it is also beneficial for aggressive individuals who are being eavesdropped on, as they also experience decreased energy expenditure from reduced fighting (Dall et al. 2004; Schuett et al. 2010). Thus, competition for mates or other resources may help generate intraindividual consistency in male aggressiveness (Schuett et al. 2010). Furthermore, females may show higher preference for males with more consistent behavior, as females may benefit from predictability of their mates (e.g. increased coordination of parental care), again resulting in selection for within individual behavioral consistency (Schuett et al. 2010).

Finally, positive feedback loops may exist between the behavior and state of an individual (i.e. features an individual must consider when making behavioral decisions to maximize fitness; McNamara & Houston 1996; Houston & McNamara 1999; Clark & Mangel 2000; Rands et al. 2003; Dall et al. 2004; Sih et al. 2004b; 2015; Luttbeg & Sih 2010; Wolf et al. 2008; Wolf & Weissing; 2010). Take, for example, a case where two individuals have the same metabolic requirements and foraging success, but one individual (Individual "A") begins with a lower energy reserve than the other (Individual "B"). When individual A's energy reserves drop below a threshold that causes the risks of starving to death to outweigh the predation risks associated with foraging alone, it leaves the safety of its shelter (Rands et al. 2003; Dall et al. 2004). Individual B will leave the safety of its shelter to forage soon after individual A, because although it is not at risk of starvation, the benefits of foraging in a pair outweigh the risks associated with foraging before required from an energetic standpoint (Rands et al. 2003; Dall et al. 2004). However, because individual B begins foraging with higher energy reserves than individual A, it can afford to return more quickly to its shelter (Rands et al. 2003; Dall et al. 2004). Furthermore, because individual A has now increased its energy reserves to a point where the risks of foraging alone outweigh the risks of starvation, it will soon follow individual B back to shelter, even though its energy reserves are still relatively low compared to those of individual B (Rands et al. 2003; Dall et al. 2004). In this scenario, the internal state of individual A creates a situation where it will always begin foraging slightly before and end foraging slightly after individual B, prompting it to become the riskier individual in the pair and confining its flexibility in risk taking (Rands et al. 2003; Dall et al. 2004). In this way, the state of an individual can maintain intraindividual consistency in risk taking behavior (Dall et al. 2004). Furthermore, the individuals' current decisions, dictated by their personalities, affect their future states, which, in turn, reinforce intraindividual consistency in behavior, thus generating a positive feedback loop between behavior and internal state (Dall et al. 2004).

Measuring animal personality

The first step in any study on interindividual variation is to quantify the trait of interest. Common measures of animal personality include consistent interindividual differences in boldness, exploration behavior, and aggression (e.g. Reichert & Hedrick 1993; Maupin & Riechert 2001; Banks et al. 2002; Sundström et al. 2004; Sih & Watters 2005; 2014; Dingemanse et al. 2007; Reaney & Backwell 2007; Pike et al. 2008; Colléter & Brown 2011; Dahlbom et al. 2011; Pruitt & Ferrari 2011; Pruitt & Riechert 2011; Schuett et al. 2011; Betini & Norris 2012; Favati et al. 2014; Le Cœur et al. 2015; Pruitt et al. 2019). While behavior is moderately flexible within an individual, the range of a behavior that an individual displays is often constrained. For example, certain individuals consistently show relatively higher levels of aggression compared to conspecifics (e.g. Sih & Watters 2005; 2014; Dingemanse et al. 2007; Colléter & Brown 2011; Pruitt & Ferrari 2011; Pruitt & Riechert 2011; Betini & Norris 2012). Personality is typically measured using assays designed to record specific behaviors in a certain context. For example, exploration behavior is often assessed by placing an individual in a novel arena and recording measures related to how it explores the environment (i.e. how much of the arena it visits, how quickly it visits various portions of the arena, etc.; e.g. Verbeek et al. 1994; Dingemanse et al. 2002; Quinn et al. 2009; Schuett et al. 2011; Favati et al. 2014). In these assays, individuals are often tested in isolation, however, this is not always the case. For example, recently scientists have become interested in measuring social personality traits, using social network analyses and observing interindividual consistency and between individual variation in an individual's network position (i.e. how social it is; Wilson et al. 2013). Regardless of whether or not an individual is tested in isolation, however, for personality to exist, behavioral traits must be consistent within the individual and variable across individuals (i.e. repeatable). Thus, behavioral assays must be conducted multiple times for repeatability to be examined. Repeatability is a measure of both within individual consistency as well as between individual variation, and it is often defined as the total proportion of variance explained by differences between groups (*R*; where groups are defined as individuals, when testing for individual differences in behavioral traits; Sokal & Rohlf 1995; Nakagawa & Schielzeth

2010). Furthermore, a number of studies have suggested a genetic basis of behavioral traits (Gosling 2001; Dingemanse et al. 2002; Quinn et al. 2009; Sih et al. 2004a; van Oers et al. 2004a,b; 2005). Heritability estimates the degree of variation in a phenotypic trait that is due to genetic variation between individuals in that population, and the heritability of personality can be measured as the ratio of narrow sense heritability (i.e. additive genetic variation/phenotypic variation) to repeatability (Dochtermann et al. 2015). A meta-analysis conducted on 70 estimates of narrow sense heritability and repeatability across 10 studies, found a mean narrow sense heritability of 0.14 and a mean repeatability of 0.29, yielding an estimated ratio of narrow sense heritability to repeatability of 0.52 (Dochtermann et al. 2015). This suggests that, across the studies examined, 52% of personality variation arose from additive genetic variation. If a given measure of personality has a genetic component, and if that measure also affects fitness, selective forces may act to shape the distribution of personality phenotypes within and across populations.

Under some situations, different measures of personality are correlated across a range of contexts, forming a "behavioral syndrome" (Sih et al. 2004a; b; Bell 2006). For example, a positive correlation between boldness towards predators, agonism towards conspecifics, aggressiveness towards prey, and levels of nonadaptive wasteful killing has been shown in the desert grass spider (*Agelenopsis aperta*; Reichert & Hedrick 1993; Maupin & Riechert 2001). Under other circumstances, different measures of personality have not been found to be correlated across contexts. For example, a number of studies on red junglefowl (*Gallus gallus*) and the closely related domestic fowl (*Gallus domesticus*) have found no evidence of a behavioral syndrome (Favati et al. 2014; 2016; 2018; Zidar et al. 2016). It is important to note however, that even within a single species, the existence of a behavioral syndrome may vary across time and space (Bell & Sih 2007; Dingemanse et al. 2007). For example, different populations of three-spined sticklebacks (*Gasterosteus aculeatus*) have been shown to vary in correlations between activity, aggressiveness, and exploratory behavior (Dingemanse et al. 2007). This discrepancy appears to be driven by factors related to the size and predation pressure of home ponds, with behavioral syndromes occurring in large ponds with piscivorous predators and

absent, or weak, in small ponds lacking predation (Dingemanse et al. 2007). Dingemanse et al. (2007) suggest that under certain ecological conditions, but not others, there may be advantages to correlations between these personality measures, causing selection to favor optimal combinations of behavioral traits.

Broad-scale ecological and evolutionary consequences of personality

Personality may have several broad-scale ecological and evolutionary consequences. For example, consistent differences in behavior between individuals have the potential to affect how well populations and species respond to natural or anthropogenic environmental change (Dall et al. 2004; Sih et al. 2004b). In general, reactive individuals may be better able to cope with changing environments, while proactive individuals may have more difficulty breaking set routines (Verbeeket al. 1994; 1996; Koolhaas et al. 1997; Sih et al. 2004b). This can have important consequences for populations subjected to natural disasters or human disturbance. Furthermore, if the evolution of personality traits is tied to the evolution of other traits, such as those related to morphology, interindividual differences in behavior could enable speciation (Wcislo, 1989; Wilson et al., 1994; Dall et al. 2004; Ingley & Johnson 2014). Bold and aggressive individuals may be more prone to dispersal and more likely to disperse to areas different from that of the source population, compared to their shy or less aggressive counterparts (Duckworth & Badyaev 2007; Cote et al. 2010; Sih et al. 2012; Ingley & Johnson 2014). If fitness consequences related to personality are habitat dependent (i.e. some personality types are favored in certain habitats while others are favored in different habitats), selective pressures acting on founding populations may differ in directionality from those acting on source populations, resulting in divergence between populations, and potentially impacting reproductive isolation (Ingley & Johnson 2014). Additionally, reproductive isolation may arise as a result of assortative mating and/or divergent selection, also leading to speciation (Both et al. 2005; Ingley & Johnson 2014). Lastly, speciation may occur if individuals with different personality types exhibit different temporal or spatial patterns, causing more interactions to occur between individuals

with similar personality types than those with dissimilar personality types, ultimately leading to reproductive isolation (Cote et al. 2010; Ingley & Johnson 2014). It is clear that personality can shape ecology and evolution across various scales, and a deeper understanding of the causes and consequences of personality is required.

Personality in a social context

Personality has been demonstrated to influence the frequency, strength, nature, and outcomes of social interactions. For example, personality may affect with whom individuals associate (e.g. Pike et al. 2008), with whom they mate (Schuett et al. 2010), and communication among individuals (e.g. Matessi et al. 2010). Furthermore, personality has been shown to influence social dominance in a number of species, though results are mixed concerning the directionality of such relationships. For example, in ornate tree lizards (*Urosaurus ornatus*) shyer males may attain a higher status than bolder males (Taylor & Lattanzio 2016). In contrast, in species such as male rainbow fish (*Melanotaenia duboulayi*), brown trout (*Salmo trutta*), and zebrafish (*Danio rerio*), bolder individuals may be more dominant (Sundström et al. 2004; Colléter & Brown 2011; Dahlbom et al. 2011). Similar contrasts have been found to occur for other measures of personality. For example, slower-exploring male mountain chickadees, (*Poecile gambeli*) may dominate faster explorers (Fox et al. 2009), while faster-exploring female zebra finches (*Taeniopygia guttata*) may dominate slower explorers (David et al. 2011). Personality has also been shown to affect an individual's position in a social network (Pike et al. 2008; Croft et al. 2009; Godfrey et al. 2012; Tanner & Jackson 2012; Aplin et al. 2013). For example, in three-spined sticklebacks, shy fish have greater numbers of associations than bold individuals, but shy fish preferentially associate with fewer conspecifics, whereas bold individuals distribute their associations more equally across groupmates (Pike et al. 2008). In addition to influencing interactions between conspecifics, personality may also affect interactions between heterospecifics (Webster *et al.* 2009; Pruitt & Ferrari 2011; Pruitt *et al.* 2012). For example, depending on the composition of personality types of *Anelosimus studiosus* in mixed species social spider

colonies, interspecific interactions can take the form of an ammensalism, commensalism, or mutualism (Pruitt & Ferrari 2011).

It is important to note that the effects of personality on social interactions at the individual level may feed back to affect emergent group level properties (Sih and Watters 2005; Pike et al. 2008; Pruitt & Ferrari 2011; Pruitt & Riechert 2011). For example, if personality influences how social an individual is (i.e. its network position), the composition of individuals with certain personality types in a group (i.e. group phenotypic composition) should feed back onto group level network structure (Pike et al. 2008). Similarly, measures of group personality composition, such as mean personality composition or the presence of an individual with a given personality type, can affect the number of social and/or sexual interactions occurring in a group as a whole. For example, in water striders (*Aquarius remigius*), group level mating performance (i.e. the number of successful matings observed in a group) is reduced when a group contains one or more hyper-aggressive males (Sih & Watters 2005). Although recent work suggests that personality may play a large role in group dynamics (Sih and Watters 2005; Pruitt & Ferrari 2011; Pruitt & Riechert 2011), little has been done to examine this relationship thus far.

Selective forces acting on personality

Given its influence on the nature and outcomes of social interactions, personality can have important fitness consequences for individuals. Personality has been shown to affect survival and/or reproduction in many species (reviewed in Dingemanse & Réale 2005; Smith & Blumstein 2008). For example, more aggressive male tree swallows (*Tachycineta bicolor*) and faster-exploring female blue tits (*Cyanistes caeruleus*) have been shown to fledge more chicks than their less aggressive or slower-exploring counterparts (Betini & Norris 2012; Mutzel et al 2013). Similarly, shyer guppies (*Poecilia reticulata*) and faster-exploring sibling voles (*Microtus rossiaemeridionalis*) were found to have higher survival than bolder or slower-exploring individuals (Dugatkin 1992; Banks et al. 2002).

Although the effects of personality in natural selection have received a considerable amount of attention (reviewed in Dingemanse & Réale; 2005), the effects of personality in sexual selection have received far less consideration (reviewed in Schuett et al. 2010), and a major gap in personality research involves understanding the effects of personality on reproductive success. Sexual selection arises from differential reproductive success generated by intrasexual competition for mates and/or fertilization of gametes (Darwin, 1871; Andersson 1994). Because females are often the limiting sex, sexual selection is typically stronger in males (Darwin, 1871; Bateman 1948; Trivers 1972; Andersson 1994). Competition among males can occur via both precopulatory (i.e. number of mates) and postcopulatory mechanisms (i.e. paternity share – the proportion of the eggs of a male's partner(s) that he fertilizes in relation to those fertilized by his competitors), in systems where females mate multiply (i.e. polyandry; Parker 1970; Kokko et al. 2006; Parker and Birkhead 2013; Firman et al. 2017). Furthermore, males may gain a mating advantage via intrasexual competition (male-male competition) or female choice (Darwin, 1871; Trivers 1972; Andersson 1994). While it is obvious how sexual selection functions in promiscuous systems, in socially monogamous systems, males may increase mating performance via extrapair pair paternity. More than 70% of socially monogamous avian species have been found to engage in extrapair copulations, with an average of ca. 11% extrapair young in an average of ca. 19% of broods (Griffith et al. 2002). Superb fairy wrens (*Malurus cyaneus*) exhibit the highest known rate of extrapair paternity, with 76% of offspring in groups being sired by extrapair fathers (Mulder et al. 1994).

Individuals with certain personalities may be more successful at acquiring mates than others as result of intersexual or intrasexual selection (Schuett et al. 2010). On one hand, females may favor males with certain personality traits. For example, it has been demonstrated that moderately and highly-exploratory female zebra finches exhibit a preference for exploratory over unexploratory males (though no preference was shown by less exploratory females; Schuett et al. 2011). On the other hand, males with certain personalities may gain increased access to mates, if they perform better in male-male competition. For example, bolder, more aggressive, and more active males are more likely to be

dominant in rainbow fish (*Melanotaenia duboulayi*), and status is closely tied to reproductive success in this species (Colléter & Brown 2011). Discrepancies in fitness between individuals with different personality types may arise as a result of differences in quality (e.g. genetic quality and/or ability), as certain behaviors may be more costly to express (Schuett et al. 2010). For example, fast-exploring individuals may expend more energy and bold individuals may incur more risks than slow-exploring or shy individuals, respectively (Schuett et al. 2010). Thus, quality may be positively correlated with exploration behavior and boldness, leading to a relationship between personality and fitness. Furthermore, males with certain personality types may gain a competitive advantage over other males, or enjoy heightened female preference, if their personality causes them to display particular behaviors or physiological responses (Verbeek et al. 1999; Cockrem 2007; Reaney & Backwell 2007). For example, bolder male fiddler crabs (*Uca mjoebergi*) court females more, and may enjoy heightened female preference and mating performance as a result (Reaney & Backwell 2007).

In addition to the fitness consequences associated with an individual's own personality, the personalities of the conspecifics in an individual's social environment (i.e. potential mates and competitors) may affect an individual's fitness directly, or indirectly, through interactions with the focal individual's phenotype, to affect fitness. For example, in great tits (*Parus major*), fledgling condition may be influenced by an interaction between the breeding male's and female's exploration behaviors, with assortative pairs at both extremes producing fledglings that enjoy higher nestbox-specific mass (Both et al. 2005). Both et al. (2005) have hypothesized that individuals at both extremes of the exploration spectrum may be of higher quality than intermediate individuals, with faster explorers excelling at obtaining/defending better territories and slower explorers providing better parental care or producing better chicks. Similarly, the personality composition of an individual's competitors also has the potential to influence an individual's fitness. For example, in water striders, individual males have depressed mating success when at least one of their group mates is a hyper-aggressive male (Sih et al. 2014). Likewise, in the social spider *Anelosimus studiosus*, females have been shown to have lower survival and fecundity when in groups composed of all aggressive or all

docile females than when in heterogenous groups (Pruitt and Ferrari 2011; Pruitt and Riechert 2011). Although, fitness consequences may arise as a result of the personality of one's self, one's competitors, one's actual/potential mates, or a combination of these factors, most work to date has focused solely on the fitness effects of a focal individual's own personality. Thus, there is a substantial gap in knowledge regarding the role of an individual's social environment in shaping selective forces and modulating relationships between an individual's personality and its reproductive performance.

Maintenance of interindividual behavioral variation

Although we know that personality can have large impacts on fitness, questions remain about the maintenance of interindividual variation in behavior (Dall et al. 2004; Dingemanse & Réale; 2005; Wolf & Weissing 2010; Schuett et al. 2010). Several non-mutually exclusive hypotheses have been put forward in explanation. First, it is possible that between individual variation in behavior simply reflects externally induced state differences (Wolf & Weissing 2010). For example, stochastic processes such as differences in environmental conditions during a critical developmental period, disease outbreaks, etc. may generate state differences between individuals, and such state differences may cause individuals to behave differently in an effort to maximize fitness. In this case, interindividual variation in behavior reflects phenotypic plasticity, rather than a genetic polymorphism, and individuals with different phenotypes do not need to attain identical fitness for personality to be maintained, as interindividual behavioral differences simply arise as a result of external variation (Wolf & Weissing 2010).

Second, life history tradeoffs between processes such as growth and mortality or current and future reproduction may be tied to personality traits, maintaining interindividual variation in behavior (Lima 1998; Biro et al. 2004; 2006; Stamps 2007; Wolf et al. 2007; Biro & Stamps 2008; Dammhahn 2012). If individuals excel in some arenas but do poorly in others (e.g. if individuals with a given personality type experience higher survival while individuals with the opposite personality type experience higher reproduction), then both phenotypes will continue to persist in the population. For

example, in grey mouse lemurs (*Microcebus murinus*), older males may have high current but low expected future reproductive output, given high mortality rates, while younger males may have low current reproductive performance due to their small size, but higher future reproductive output, if they can survive past their first year (Dammhahn 2012). Boldness is a risky strategy, and younger individuals should benefit from being less bold, as it should increase their probability of survival, and thus, future reproduction. In contrast, older individuals should invest more heavily in current reproduction and would therefore benefit from being bolder. Dammhahn (2012) found that older male lemurs were bolder than younger individuals, suggesting a life history tradeoff associated with boldness between current and future reproduction in this species (Dammhahn 2012).

Third, fluctuating selection, resulting from spatial and/or temporal environmental heterogeneity, could facilitate the maintenance of interindividual behavioral variation (Dingemanse et al. 2004; Cote et al. 2008; Quinn et al. 2009; Harris & Siefferman 2014; Galliard et al. 2015; Le Cœur et al. 2015; Nicolaus et al. 2016; but see Bergeron et al. 2013). For example, in years with poor food availability, bolder eastern chipmunks (*Tamias sibiricus*) were found to have higher annual reproductive success than shyer individuals, while shyer individuals had higher annual reproductive success compared to bolder individuals in years where food was abundant (Le Cœur et al. 2015). In addition to fluctuations in an individual's physical environment, variation in an individual's social environment could also help maintain personality (Cote et al. 2008; Quinn et al. 2009; Harris & Siefferman 2014; Galliard et al. 2015; Nicolaus et al. 2016). For example, when conspecific density was higher, Cote et al. (2008) found that less social common lizards (*Zootoca vivipara*) had higher survival than more social individuals, and vice versa (but see Galliard et al. 2015 where survival was not affected by an interaction between boldness and density in this species). It is important to note that variation in an individual's interspecific social environment could also work to maintain personality, however, limited work has been conducted to explore this possibility (but see Harris & Siefferman 2014).

Fourth, non-equilibrium dynamics could also maintain interindividual behavioral differences (Wolf & Weissing 2010). For example, behavioral types that are good at dispersing and colonizing new areas (i.e. dispersers) are likely to see fitness gains in unoccupied environments and fitness losses in heavily inhabited environments (Duckworth & Kruuk 2009; Wolf & Weissing 2010). In contrast, behavioral types that are not good at dispersing and colonizing (i.e. non-dispersers) may experience the opposite pattern. Under stochastic environmental perturbations, such as a wildfire that frees up space, dispersers may experience a rapid increase in fitness as they colonize the newly available area, followed by a fitness decline once the area becomes heavily inhabited, thus promoting more favorable conditions for non-dispersers (Wolf & Weissing 2010).

Fifth, disruptive selection could maintain interindividual variation in behavior if individuals with extreme personalities experience higher survival and/or reproduction compared to individuals with intermediate phenotypes (Dingemanse et al. 2004; Bergeron et al. 2013). For example, in adult, but not juvenile, eastern chipmunks, patterns suggesting strong disruptive selection were seen, with extreme explorers experiencing nearly double the survival observed in intermediate-exploring individuals over a six-month period (Bergeron et al. 2013). Individuals with extreme personalities may have different, but equally successful, strategies for increasing survival or reproduction, while intermediate personality types may not enjoy the fitness advantages gleaned from fully committing to a particular strategy. For example, in the case of eastern chipmunks, slower explorers may have low mortality because they spend more time in the security of their burrows, while faster explorers may also enjoy low mortality, as their high levels of exploration permits them increased information about their environment, including the locations of various refuges (Bergeron et al. 2013).

Sixth, although positive frequency dependent selection is expected to erode interindividual variation, if an individual has higher fitness when surrounded by competitors with dissimilar personalities, negative frequency dependent selection may maintain interindividual variation in personality (Dall et al. 2004; Wolf & Weissing 2010). For example, in the social spider, *Stegodyphus dumicola*, bold colonies were demonstrated to be more fecund than shy colonies when inhabiting

neighborhoods where shy colonies were more common than bold colonies, suggesting negative frequency dependence (Pruitt et al. 2019). Negative frequency dependence may occur via a couple of general channels. Rare phenotypes may have a competitive advantage, given that rarer phenotypes may exploit different strategies in a resource limited environment, reducing the relative levels of competition experienced by these individuals (Wolf & Weissing 2010). Similarly, predators and pathogens often overlook rarer phenotypes, targeting more common phenotypes, due to past selection or phenotypic adaptation of traits like search image development (Wolf & Weissing 2010).

Lastly, if individuals preferentially mate with conspecifics that are behaviorally similar to themselves, assortative mating could maintain interindividual differences in personality (Schuett et al. 2010). There may be advantages to choosing a mate with a comparable personality type, given that behaviorally similar pairs may have better coordination during activities such as nest defense or food provisioning (Schuett et al. 2010). Although, like divergent selection, assortative mating could result in speciation if it occurs only among extreme pairs and if left unchecked, provided that other selective forces work, for example, to promote disassortative mating (e.g. increased survival of offspring produced by disassortatively mated pairs), then variation in personality may be maintained, without leading to speciation. However, if personality is linked to quality, high quality individuals may be more likely to mate with other high quality individuals, leaving poorer quality individuals of the opposite personality type to pair up (McNamara & Collins 1990; Johnstone,1997; Schuett et al. 2010). This type of assortative mating would instead be expected to degrade interindividual variation in personality, since high quality pairs should have elevated reproductive success, thus passing on more genes of one behavioral type, leading to directional selection (Schuett et al. 2010).

Aims of Research

Broadly, my thesis aims to examine the intersection between an individual's personality and its social environment and fill existing gaps in knowledge relating to personality's effects on sexual selection and group dynamics. I strive to understand the driving factors that assist in the maintenance

of interindividual variation in personality traits and focus on mechanisms related to negative frequency dependent selection (**Chapter 3**), assortative mating (**Chapters 2 & 3**), and heterogeneous selection (**Chapter 4**). For this work, I use a population of captive red junglefowl and a population of wild great tits to explore a variety of questions. Using this dual study system for my research proves beneficial for several reasons. First, the wild great tit study system allows me to observe how personality may affect reproductive outcomes in a natural setting, while the captive red junglefowl system permits me the freedom of controlled experimental manipulations. Second, great tits are socially monogamous, while red junglefowl embody a polygynandrous mating system. This contrast allows me to compare the effects of personality on reproductive success across disparate mating systems. Furthermore, because both great tits and red junglefowl are social species, there is ample scope to assess how competitors may affect individual fitness as well as observe the emergent group properties born from the individual personality makeup of a group.

My thesis begins by examining how the personalities of focal individuals and their mates, as well as the group personality composition of their competitors, affects focal reproductive performance in both great tits and red junglefowl (**Chapters 2 and 3**). I go on to explore how other aspects of group phenotypic composition, specifically the species composition of an individual's local social environment, modulates relationships between focal personality and reproductive performance in great tits (**Chapter 4**). I conclude by using experimentally manipulated groups of red junglefowl to assess how group personality composition affects emergent group level properties related to social patterns and structure (**Chapter 5**).

Study Species and Study Sites

Great tits have emerged as one of the primary model systems used for personality research, undergoing over two decades of personality work (e.g. Verbeek et al. 1994; 1996; Dingemanse et al. 2003; Dingemanse & de Goede 2004; van Oers et al. 2004a; 2004b; Cole & Quinn 2011; Patrick et al. 2011; Araya-Ajoy et al. 2016; Abbey-Lee et al. 2018; Firth et al. 2018). Most studies on great tit

personality have focused on exploration behavior, quantified by measures garnered from behavioral assays where an individual is observed in a novel arena. Scientists commonly employ exploration behavior as a singular measure of personality in great tits, as it is considered to be a good proxy for proactivity in this species (Carere et al. 2005; Groothuis & Carere 2005; Quinn et al. 2009 2012; Aplin et al. 2013), given evidence suggesting positive correlations with several other behavioral traits including aggressiveness, (Verbeek et al. 1996), boldness towards a novel object (Verbeek et al. 1994), and risk-taking behavior (van Oers et al. 2004a). In great tits, exploration behavior has been shown to have heritability estimates ranging from 0.22 – 0.61 and measured repeatabilities ranging from 0.27 – 0.61, across populations (Dingemanse et al. 2002; Drent et al. 2003; Quinn et al. 2009). In this species, exploration behavior has been shown to correlate with processes such as natal dispersal (Dingemanse et al. 2003; Quinn et al. 2011b), dominance (Verbeek et al. 1996; Dingemanse & de Goede 2004; Cole & Quinn; 2011), social network position (Aplin et al. 2013), foraging (Quinn et al. 2011a), collective behavior (Aplin et al. 2014), and reproductive success and strategy (van Oers et al. 2008; Patrick et al. 2011; Araya-Ajoy et al. 2016; Abbey-Lee et al. 2018; Firth et al. 2018). However, it is important to note that the consequences of exploration behavior may vary with age or sex in great tits. For example, faster-exploring territorial males have been shown to dominate their slower-exploring counterparts, while slower-exploring non-territorial juvenile males have been shown to dominate their faster-exploring counterparts (Dingemanse & de Goede 2004). Similarly, exploration behavior may affect male, but not female, extrapair relations (Patrick et al. 2011; but see van Oers et al. 2008).

There has been a long-term monitoring project on great tits in Wytham Woods, Oxfordshire, UK since 1947. Studying this wild population allows me to examine how personality affects social interactions and fitness using a long-term breeding dataset. In the spring, great tits form socially monogamous pairs that defend breeding territories from conspecific neighbors, in addition to nesting alongside blue tits, and both intra- and interspecific competition have been shown to affect great tit reproductive performance (Minot 1981; Minot & Perrins 1986; Wilkin et al. 2006; Dhondt 2012).

Approximately 13% extrapair paternity has been recorded in Wytham great tits, and previous work has shown that the personalities of the breeding male and female in a pair can influence patterns of extrapair paternity and/or within pair paternity in both Wytham great tits as well as in other populations of great tits (van Oers et al. 2008; Patrick et al. 2011; Araya-Ajoy et al. 2016; Abbey-Lee et al. 2018). Questions remain, however, as to whether the personalities of individuals in neighboring territories affect male promiscuity. Assessing whether neighborhood personality composition affects individual reproductive success allows us to examine the potential effects of social selection on personality. Furthermore, questions remain as to how other aspects of an individual's breeding environment, such as the local species composition, may modulate relationships between focal personality and reproductive performance.

Compared to great tits, far fewer studies have explored the consequences of, and mechanisms maintaining, personality in red junglefowl. Furthermore, in contrast to great tits, many repeatable behavioral traits are uncorrelated in red junglefowl, as well as in the closely related domestic fowl, suggesting a lack of a behavioral syndrome (Favati et al. 2016; 2018; Zidar et al. 2016). Personality has been shown to relate to things like learning speed (Zidar et al. 2018) and dominance (Favati et al. 2014, Favati et al. 2017), however.

For more than a decade, the Pizzari Lab has kept a captive population of red junglefowl at the John Krebs Field Station in Wytham Woods. Although no work has been published on personality in this population, its captive nature makes it ideal for experimentally manipulating group personality composition in a controlled environment. Red junglefowl form tightly structured same-sex dominance hierarchies, and social status often predicts mating success (Collias et al. 1994; Collias & Collias; 1996; Kim & Zuk 2000). Questions remain regarding how the personality of individuals, their competitors, and their potential mates may predict male mating performance and/or strategy in red junglefowl. Furthermore, questions remain regarding how group personality composition may affect emergent group properties such as social network structure.

Outline of the Thesis

In **Chapter 2**, I focus on exploring whether the age and personality of a focal individual, and the mean age and personality of conspecifics in the focal individual's breeding neighborhood, affect extrapair paternity and cuckoldry in great tits. Previous studies suggest that focal age (Kempenaers et al. 1997; Perreault et al. 1997; Pilastro et al. 2002; Lubjuhn et al. 2007; Hill et al. 2011; Cleasby and Nakagawa 2012; Hsu et al. 2015 Araya-Ajoy et al. 2016; but see Abbey-Lee et al. 2018) and/or personality (van Oers et al. 2008; While et al. 2009; Patrick et al. 2011; Araya-Ajoy et al. 2016; Bókony et al. 2017; but see McCowan et al. 2014) may affect extrapair paternity and/or cuckoldry in a number of species including great tits, however, no studies have examined how the mean phenotypic composition of the local social environment within which an individual breeds affects fitness gains or losses related to extrapair paternity.

Following **Chapter 2**, I go from exploring the reproductive consequences of focal and competitor personality in a species with a socially monogamous mating system, to examining these questions using a species with a more complex polygynandrous mating system. **Chapter 3** explores the effect of sexual selection on two personality traits in red junglefowl: 1) exploration and 2) boldness. Although previous research suggests that personality may play a role in male mating performance across a variety of species (Reaney & Backwell 2007; Réale et al. 2009; Colléter & Brown 2011; Sih et al. 2014; Araya-Ajoy et al. 2016), it is still unclear whether sexual selection could maintain interindividual variation in behavior. I assess whether a focal male's exploration and boldness affects pre- and postcopulatory measures of male mating performance, mating strategy, and female preference using experimentally engineered mixed-sex groups consisting of different ratios of individual personality types. Furthermore, I examine how mean male competitor personality influences relationships between focal male personality and reproductive performance, and I test specifically for evidence of negative frequency dependent sexual selection.

Continuing forward, I assess how aspects of the group phenotypic composition of an individual's social environment, other than group personality composition, may affect relationships

between focal personality and reproductive performance. **Chapter 4** investigates whether the reproductive performance of individual great tits of different ages and with different personality types is differentially affected by varying levels of competitive pressure, measured as the ratio of neighboring blue tits (*Cyanistes caeruleus*) to great tits (i.e. local species composition). Past work has suggested a reduced effect of inter- versus intraspecific competition on great tit reproductive success (Wilkin et al. 2006; Dhondt 2012). If increased proportions of blue tits in the local social environment relaxes competitive pressure on great tits, this may create greater similarity or dissimilarity in fitness between individuals with different phenotypes, or certain phenotypes may be favored under higher versus lower competition and vice versa (Clutton-Brock et al. 1987; Festa-Bianchet et al. 1998; Bonenfant et al. 2002; Cote et al. 2008; Le Galliard et al. 2015; Nicolaus et al. 2016). In this way, personality traits may be maintained by variation in local species composition over space or time (i.e. heterogeneous selection).

Lastly, I move away from examining the individual level consequences of personality to explore how group personality composition affects group level social dynamics. Past work suggests that group phenotypic composition can affect emergent group properties in a couple of invertebrate species (Sih & Watters 2005; Pruitt and Ferrari 2011; Pruitt and Riechert 2011). Furthermore, social network structure underlies many important processes such as disease transmission and information flow, ultimately holding the potential to influence group level fitness. Given this, it is important to understand how the individual phenotypic makeup of a group may cause variation in social patterns and structure. **Chapter 5** examines whether group exploration behavior and boldness composition relate to social patterns and network structure in red junglefowl. I record the occurrence of male sexual harassment of females, intrasexual aggressive interactions, and intra- and inter-sexual allopreening interactions across 24 groups of red junglefowl with experimentally manipulated group personality compositions. I explore whether group exploration and boldness composition predict the mean number of each interaction type observed in a group, as well as the network structure of social networks based on these interactions.

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Chapter 2

Partner's age, not social environment, predicts extrapair paternity in wild great tits (*Parus major*)

Partner's age, not social environment, predicts extrapair paternity in wild great tits (*Parus major*)

Abbreviated Title: Individual and neighborhood effects on extrapair paternity

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Lay Summary

Mating activity may be influenced by the traits of one's self, one's partner, or one's social environment. Males increase the number of genes they pass on by mating with females other than their partner. We show that, in great tits, males are more likely be unfaithful to an older partner, and males typically breed with extrapair females whose nests are closer. Interestingly, the average age and/or personality of a male's neighbors did not influence his extrapair paternity.

Abstract

An individual's fitness is not only influenced by its own phenotype, but by the phenotypes of interacting conspecifics. This is likely to be particularly true when considering fitness gains and losses caused by extrapair matings, as they depend directly on the social environment. While previous work has explored effects of dyadic interactions, limited understanding exists regarding how group-level characteristics of the social environment affect extrapair paternity (EPP) and cuckoldry. We use a wild population of great tits (*Parus major*) to examine how, in addition to the phenotypes of focal parents, two neighborhood-level traits – age and personality composition – predict EPP and cuckoldry. We used the well-studied trait "exploration behavior" as a measure of the reactive-proactive personality

axis. Because breeding pairs inhabit a continuous "social landscape", we first established an ecologically relevant definition of a breeding "neighborhood" through genotyping parents and nestlings in a 51-ha patch of woodland and assessing the spatial predictors of EPP events. Using the observed decline in likelihood of EPP with increasing spatial separation between nests, we determined the relevant neighborhood boundaries, and thus the group phenotypic composition of an individual's neighborhood, by calculating the point at which the likelihood of EPP became negligible. We found no evidence that "social environment" effects (i.e. neighborhood age or personality composition) influenced EPP or cuckoldry. We did, however, find that a female's own age influenced the EPP of her social mate, with males paired to older females gaining more EPP, even when controlling for the social environment. These findings suggest that partner characteristics, rather than group phenotypic composition, influence mating activity patterns at the individual level.

Keywords: group phenotypic composition, social environment, exploration behavior, reproductive success, spatial autocorrelation

Introduction

An individual's fitness is a product of its own phenotype as well as the phenotypes of others in its social environment. Indeed, dyadic interactions in many contexts, such as competitive, cooperative, or sexual interactions, may be fundamental components of individuals' survival and reproduction (e.g. Ekman 1990). Furthermore, group-level attributes (i.e. in relation to the local social environment or neighborhood) can impact the fitness of the individuals within it (Goodnight et al. 1992; Moore et al. 1997; Wolf et al. 1999). For example, in the social spider *Anelosimus studiosus*, females have been shown to experience higher fitness when in groups containing a mix of aggressive and docile phenotypes than when in groups composed of all aggressive or all docile individuals (Pruitt and Ferrari 2011; Pruitt and Riechert 2011).

Group phenotypic composition is a term used to encompass any descriptor of a group's phenotypic makeup including averages, variance, and the presence or absence of a certain phenotype in a group (Pruitt and Riechert 2011; Pruitt and Ferrari 2011). In addition to representing the assortment of individual phenotypes, group phenotypic composition may also reflect an emergent group property (e.g. the mating system) that cannot be traced back to the phenotypes of constituent individuals (Smaldino 2014). Group phenotypic composition may refer to any phenotypic trait such as body size, age, or personality and can affect success both at the group and individual level (Farine et al. 2015). Furthermore, the phenotypic composition of a group does not necessarily affect all members of a group equally, since interactions may exist between group phenotypic composition and an individual's phenotype. For example, in large groups of visually similar organisms, individuals with the common phenotype may benefit from the confusion effect, reducing their chances of predation, whereas individuals with rare phenotypes may be more conspicuous to predators (Landeau and Terborgh 1986; Rodgers et al. 2014). Group phenotypic composition has been shown to influence many processes, including foraging (Dyer et al. 2008; Pruitt and Riechert 2009, 2011; Keiser and Pruitt 2014; Laskowski and Bell 2014), predator-prey interactions (Landeau and Terborgh 1986; Rodgers et al. 2014), and host-parasite interactions (Anderson et al. 1992; Lloyd-Smith et al. 2005; Paull et al. 2012).

The effects of group phenotypic composition on fitness components are relatively understudied, however, it is reasonable to assume that fitness gains and losses relating to extrapair paternity (EPP) may be particularly influenced by group phenotypic composition, as rates of EPP are governed by interactions in the local social environment. In over 70% of socially monogamous avian species, individuals seek copulations outside of the social pair bond, resulting in EPP (Griffith et al. 2002). EPP allows males to increase fitness by increasing reproductive output, while females who engage in extrapair copulations may gain direct benefits, fertility insurance, or genetic benefits through extrapair copulations (Griffith et al. 2002). Males that are cuckolded (i.e. lose paternity to an extrapair male) will not only suffer fitness reduction due to paternity loss, but in systems with biparental care,

will suffer the cost of investing energy to raise unrelated young. A female whose social partner engages in extra-pair copulations may also suffer costs, such as decreased male investment, increased sperm depletion of her social mate, and increased risk of disease (Petrie and Kempenaers 1998). Both EPP and cuckoldry may be affected by the phenotypes of a focal individual, its social mate, potential extrapair mates, and competitors. Therefore, although seldom done, questions addressing EPP should consider all four parties (Arnqvist and Kirkpatrick 2005; Akçay and Roughgarden 2007).

Previous work has shown that the social environment can modulate access to extrapair mates, and therefore EPP rates, via breeding synchrony, breeding density, or territory configuration (Chuang et al. 1999; Richardson and Burke 2001; Thusius et al. 2001; Charmantier and Perret 2004; Taff et al. 2013; Bain et al. 2014). However, these forms of group phenotypic composition are group level properties, rather than measures describing phenotypes of a group's members, and there remains no general understanding of how the individual phenotypic makeup of a group may influence fitness gains and losses associated with EPP.

One aspect of group phenotypic composition that has received much recent attention is group personality composition. Animal personality can be defined as stable inter-individual differences in behavior, such as variation in boldness, exploration behavior, or aggression, that remain consistent over multiple contexts (Dall et al. 2004; Sih et al. 2004; Bell et al. 2009). Personality often has a considerable genetic component (reviewed in Dingemanse and Réale 2005; Dochtermann et al. 2015). Group personality composition has been shown to affect individual or group reproductive success in social spiders (*Anelosimus studiosus*; Pruitt and Ferrari 2011; Pruitt and Riechert 2011) and water striders (*Aquarius remigis*; Sih and Watters 2005; Sih et al. 2014; Wey et al. 2015). For example, in water striders, both individual and group-level mating success are reduced when at least one hyper-aggressive male is present in a group (Sih and Watters 2005; Sih et al. 2014; Wey et al. 2015). Although, to date, no work has examined potential links between group personality composition and EPP, at an individual or dyadic level, behavioral differences may influence the occurrence of EPP and cuckoldry, and several studies have suggested an effect of personality on EPP or cuckoldry (van Oers

et al. 2008; While et al. 2009; Patrick et al. 2012; Bókony et al. 2017; but see McCowan et al. 2014). For example, in White's skinks (*Egernia whitii*), less aggressive females have fewer young sired by extrapair fathers compared to more aggressive females (While et al. 2009). Thus, it seems reasonable that group personality composition may also influence patterns of EPP and cuckoldry.

Group age composition is another potentially important factor that may influence EPP and cuckoldry patterns. Although there have been no studies to suggest an effect of group age composition on reproductive success, when examining the consequences of phenotypic variation at an individual or dyadic level, age has been shown to affect EPP and/or cuckoldry in several avian species (Kempenaers et al. 1997; Perreault et al. 1997; Pilastro et al. 2002; Lubjuhn et al. 2007; Hill et al. 2011; Cleasby and Nakagawa 2012; Hsu et al. 2015). Depending on the species, the relationship between male age and cuckoldry may be positive (Hill et al. 2011), negative (Perreault et al. 1997; Pilastro et al. 2002; Lubjuhn et al. 2007), or nondetectable (Kempenaers et al. 1997). Additionally, meta-analyses indicate a positive correlation between male age and EPP gained (Cleasby and Nakagawa 2012; Hsu et al. 2015). Several suggestions have been proposed to explain why older males may be more likely to gain EPP including 1) age differences in male mating behavior (i.e. younger males may be outcompeted by older males for extrapair copulations or older males may be better at forcing or coercing females into extrapair copulations; Weatherhead and Boag 1995; Wetton et al. 1995; Hsu et al. 2017), 2) higher female propensity to engage in extrapair copulations with older males (i.e. females may prefer to mate with older males; Sundberg and Dixon 1996; Tarof et al. 2011), or 3) post copulatory mechanisms (i.e. sperm competition is enhanced in older males; González-Solís and Becker 2002, Girndt et al. 2018).

Although no studies have shown a link between female age and EPP of her social mate, previous research has suggested that female age may affect cuckoldry within the focal nest (Lubjuhn et al. 2007; Ramos et al. 2014; Moreno et al. 2015; but see Abbey-Lee et al. 2018). Younger females may be more likely to willingly engage in, or be coerced into, extrapair copulations (Moreno et al. 2015). Indeed, in pied flycatchers (*Ficedula hypoleuca*), female age has been shown to be negatively correlated with the proportion of extrapair young in a brood (Moreno et al. 2015). Similarly, female

age has been shown to interact with the age of her social mate to predict cuckoldry in blue-footed boobies (*Sula nebouxii*; Ramos et al. 2014).

In this study, we use a population of great tits (*Parus major*) to examine how EPP and cuckoldry is influenced by the phenotypes of the parents at the focal nest, as well as the individual phenotypic makeup of a group. In great tits, exploration behavior is positively correlated with boldness and aggression (Verbeek et al. 1994, 1996; Gosling 2001), forming a proactive-reactive personality axis. Thus, exploration behavior is believed to be a good proxy for proactivity in great tits (Carere et al. 2005; Groothuis & Carere 2005; Quinn et al. 2009; Cole & Quinn 2012; Aplin 2013). We specifically examined the effects of group phenotypic composition in relation to age and exploration behavior on EPP and cuckoldry, given that these two phenotypic traits have been heavily studied, relative to others, and have been repeatedly shown to affect reproduction at an individual or dyadic level in great tits (Perrins 1965; Perrins & Moss 1974; Perrins & McCleery 1985; Lubjuhn et al. 2007; van Oers et al. 2008; Patrick et al. 2012; Bókony et al. 2017; Firth et al. 2018; Araya-Ajoy et al. 2016; Abbey-Lee et al. 2018). For example, there is some evidence to suggest that male EPP may be positively correlated with male age, while cuckoldry may be negatively correlated with both male and female age (Lubjuhn et al. 2007; Araya-Ajoy et al. 2016; Abbey-Lee et al. 2018). Furthermore, males paired with faster exploring social mates have been shown to be more likely to gain EPP in our study population, while slower exploring males have been shown to sire more within pair young and fewer extrapair young than faster exploring males (Patrick et al. 2012, but see Araya-Ajoy et al. 2016 where faster exploring males have lower extrapair fertilization success in a German population of great tits). Older males may be less likely to be cuckolded due to increased experience, while, in the case of our population, faster exploring males may be more likely to gain EPP for a couple of reasons. First, they may travel further from their nest and therefore encounter a greater number of potential mates. Second, faster exploring males have been found to sample fewer potential partners before choosing a social mate, and therefore may use EPP during the breeding season to compensate for non-optimal breeding

partner choices (Firth et al. 2018). We quantified paternity using genetic markers in a subset of our study population over a 3-year period and assayed exploration behavior in a subset of parent birds.

We explored whether EPP and cuckoldry could be predicted by four traits: 1) male age, 2) female age, 3) male exploration behavior, and 4) female exploration behavior. For each trait, we examined: a) phenotype of parents at a focal nest, b) mean neighborhood phenotype, and c) relative neighborhood phenotype (measured as the interaction between the focal and mean neighborhood phenotypes). Examining relative neighborhood phenotype allowed us to explore whether the local social environment differentially affected focal individuals possessing different phenotypes. Based on past work on dyadic interactions in great tits, we predicted that individual and neighborhood age and exploration behavior would affect EPP and cuckoldry.

Methods

Study Population and Field Methods

Great tits are socially monogamous passerines with moderate rates of EPP. In Wytham Woods, Oxfordshire (51°46′ N, 1°20′ W), 12.7% - 14% of great tit nestlings have been shown to be products of EPP, with ca. 50% of broods containing extrapair young (Blakey 1994; Patrick et al. 2012; Firth et al. 2015). Wytham great tits nest primarily in permanent nestboxes, all of which have known locations. The identities of breeding males and females, date of clutch initiation (lay date), clutch size, date of egg hatching, and fledgling success have been recorded annually, under standardized protocols, for each nestbox from April - July since the 1960s, as part of a long-term monitoring project (Perrins 1965). Nestlings and parent birds that have immigrated into the study site are individually ringed.

From 2005-2007, we collected DNA sampled from all breeding adults and nestlings in a 51 ha subsection of Wytham Woods (Marley Wood and Marley Plantation; see Patrick et al. 2012). This work was conducted under Home Office License PIL30/6981 and was subject to ethical review by the Department of Zoology Local Ethical Review Committee.

Ageing breeding birds

All locally-born individuals are ringed as nestlings, and therefore their exact age is known. Birds born outside the woodland (immigrants) were aged when they were first trapped, either during the breeding season or as part of the large-scale ringing effort that takes place each winter (Voelkl et al. 2016). This was done using plumage characteristics (Svensson 1992); birds with first-year plumage are classified as yearlings (in their first year of life) and individuals first caught with adult plumage are assigned an estimated age of 2 years (Bouwhuis et al. 2009). Such approximations are not uncommon in studies dealing with ages of wild birds (e.g. Perreault et al. 1997; Lubjuhn et al. 2007). Only 6.1% of our total data and 6.8% of individuals had an estimated rather than exact age.

Personality Assays

In line with past work on great tits, we use the term "exploration behavior" as a measure of personality (e.g. Patrick et al. 2012; Aplin et al. 2013; Aplin et al. 2014; Johnson et al. 2017; Firth et al. 2018). Exploration behavior is a heritable trait that shows moderate repeatability across and between years and correlates with a range of functional behaviors in the wild in our population (Quinn et al. 2009, 2011; Cole & Quinn 2012, 2014; Aplin et al. 2013; Firth et al. 2018). We mist netted birds, or caught individuals roosting at night, and transferred them to captivity for exploration behavior assays from October-March in 2005-2010 as part of a larger study (see Quinn et al. 2009). We tested individuals singly in a novel indoor arena (length = 3.25 m, width = 4.00 m; height = 2.50 m) between the hours of 08:00 and 13:00, after housing them overnight. The novel arena consisted of five equally sized quadrats and five different surface types, including a centrally located tree in each quadrat for perching. We monitored individuals for 8 minutes following their release into the arena, and we recorded visits to each quadrat and surface type, as well as the duration of hops and flights, for a total of 12 recorded behavioral measures. We released birds at their site of capture following these assays. Individuals were tested from 1-5 times each (mean number of assays ± SD = 1.250 ± 0.593), across

seasons, with a mean ± SD of 285.9 ± 316 days between their first and last assays (see Quinn et al. 2009 for further detail).

We conducted a principal component analysis that considered the 12 recorded behaviors. We used PC1 as our measure of exploration behavior, as it described over 45% of the variation, while PC2 only described 16% of the variation, PC3 only described 11% of the variation, and PC4 – PC12 each described <10% of the variation. In addition to past work on great tits (e.g. Patrick et al. 2012; Aplin et al. 2013; Aplin et al. 2014; Johnson et al. 2017; Firth et al. 2018), studies across a wide range of species have used PC1 as their sole measure of personality (e.g. Boon et al. 2008; Starling et al. 2013; Patrick and Weimerskirch, 2014; Stanley et al. 2017). After adding the minimum value to PC1 scores, we used a square root transformation and included the transformed values in a generalized linear model which included individual, observation number, and assay date as fixed effects. We added the intercept coefficient to the parameter for a given individual, from the generalized linear model, to acquire a single exploration behavior score for each of the assayed individuals. In this way, birds with exploration behavior scores at the lower end of the spectrum can be considered slower explorers, and individuals with scores at the upper end of the spectrum can be considered faster explorers.

Genotyping and Assigning Paternity

We used a standard Chelex protocol to extract DNA (Walsh et al. 1991; Patrick et al. 2012). We genotyped all individuals at between 5-9 polymorphic microsatellite loci. We used a combined exclusion probability of >0.99 and scored each individual using GeneMapper v. 3.7 (see Patrick et al. 2012 for further details). We used MasterBayes v. 2.45 based on genetic data with Wang's genotyping error and an 80% assignment confidence (Wang et al. 2005; Patrick et al. 2012; see electronic supplementary material for details). It is important to note that, due to the set-up of this study system (and most others), it is more difficult to capture all EPP events than it is to determine whether all young in a nest were sired by the social father. For instance, our approach would have missed any EPP

events that occurred outside of our sampling area. We therefore had more confidence as to whether a male was cuckolded than we did in whether he gained EPP.

Statistical Methods

In addition to examining the effects of focal 1) male age, 2) female age, 3) male exploration behavior, and 4) female exploration behavior on EPP and cuckoldry, we examined if group means of these traits predicted whether a focal male obtained EPP or was cuckolded. To address research questions related to group phenotypic composition, a clear definition of the local social environment is needed. Defining groups is straightforward when animals live or breed in discrete units. However, in a continuous social landscape, where organisms do not form distinct groups, a challenge arises as to how to quantify a group. Individuals are limited in the space they utilize and are unlikely to interact with every individual in the population. As a result, simply examining group phenotypic composition at the population level is inappropriate (Maldonado-Chaparro et al. 2018). In socially monogamous birds, such as the great tit, breeding pairs have territories associated with a single nesting location, making it simpler to determine who individuals could potentially be interacting with (compared to individuals in free moving study systems). In this study, we defined "group" as all conspecifics in the breeding neighborhood within which a focal pair is embedded.

We explored three ways to define neighborhoods: 1) radial distance (i.e. all breeding pairs within a certain radius from the focal nest were considered neighbors), 2) nearest neighbors (i.e. all breeding pairs within x nearest nests were considered neighbors – the closest neighbor in meters was considered the first nearest neighbor, the second closest neighbor in meters was considered the second nearest neighbor, etc.), and 3) Voronoi neighbors (i.e. all breeding pairs within x breeding territories away were considered neighbors – all neighbors who shared a territory boundary with the focal nest were considered first order neighbors, all neighbors who shared a territory boundary with first order neighbors were considered second order neighbors, etc.; territory boundaries were estimated using Voronoi polygons – polygons constructed around each nestbox containing a breeding pair, whose

boundaries enclose the space closest to the nestbox contained within a given polygon, relative to all other occupied nestboxes; Aurenhammer 1991; Figure 1a).

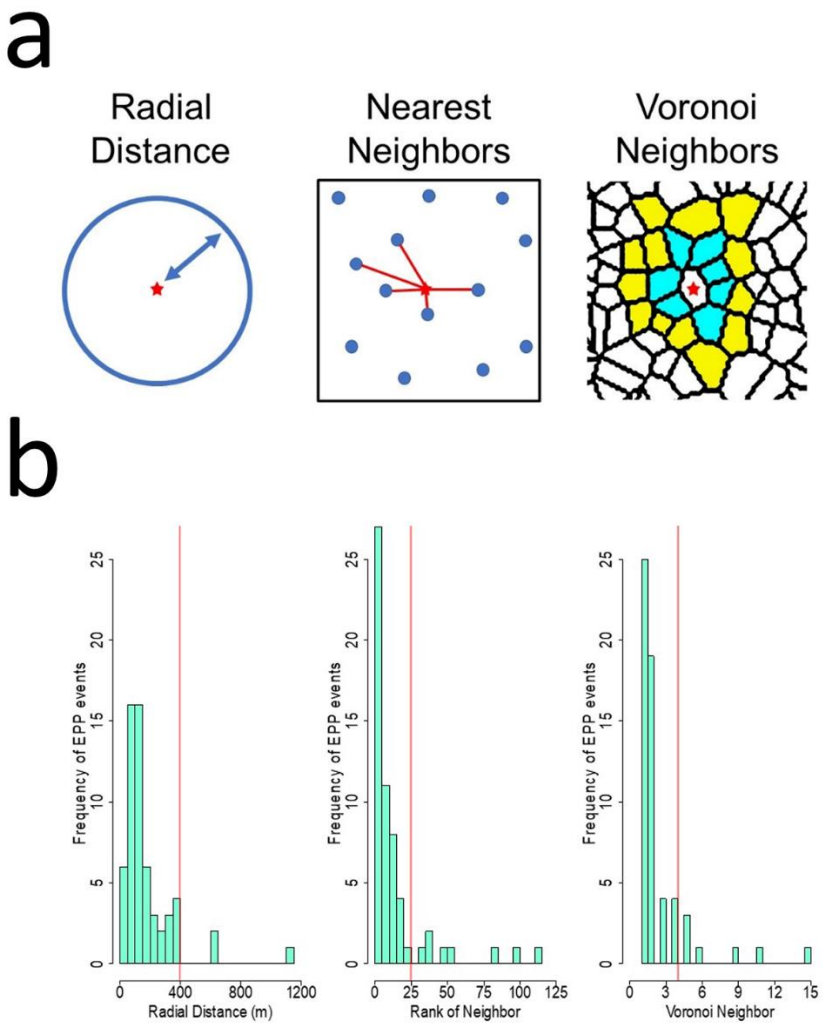

Figure 1. a) Three ways used to define neighborhoods. The red star represents the focal nest. For radial distance, all breeding pairs within the area bound by the blue circle would be considered neighbors. For nearest neighbors, if every blue dot represents a neighboring breeding pair, if we wanted to examine the five nearest neighbors, we would take the five breeding pairs closest (in meters) to the focal nest. For Voronoi neighbors, we examined how many territories away breeding pairs were from the focal nest. Here, blue highlighted territories would contain first order neighbors, while yellow highlighted territories would contain second order neighbors. **b)** Frequency distribution of recorded occurrence of EPP events (i.e. whether or not a nest contained any extrapair young) in relation to (i) neighbor distance, (ii) ranked nearest neighbors, and (iii) order of Voronoi neighbors. The vertical lines indicate the cut-offs used to define neighborhoods in further analyses (see Figure S1 for details).

We used patterns of EPP distribution to inform our decisions regarding 1) what radius to use for our measure of radial distance, 2) how many nearest nests to use for our measure of nearest neighbors, and 3) how many breeding territories (i.e. Voronoi polygons) away to use for our measure of Voronoi neighbors. This method has been utilized in previous studies examining the effects of the local breeding density and/or synchrony on EPP (Thusius et al. 2001; LaBarbera et al. 2010; Taff et al. 2013). Occurrence of EPP events (i.e. whether or not a nest contained any extrapair young) decreased as distance between the cuckolded nest (i.e. focal nest) and the cuckold's nest increased (Figures 1b and S1). Using these distributions, we defined the edge of a neighborhood as the distance from the focal nest where the probability of EPP fell below 1% (see Figure S1 and Results). Because EPP rates decreased with increasing distance (Figures 1b and S1), we weighted neighborhood means based on a neighbor's distance from the focal nest. All breeding pairs within the defined neighborhood boundaries were considered neighbors, regardless of whether they bred synchronously with the focal pair. Past work on our population suggests spatial synchrony in breeding time is correlated with local environmental phenological events (Hinks et al. 2015).

Models

Within each definition of "neighborhood" and for each of the four traits (male age, female age, male exploration behavior, and female exploration behavior), we ran a generalized linear mixed model with a binomial family and response variables of whether the focal male obtained EPP and whether the focal nest contained extrapair young. We used R 3.3.2 for all analyses (R Core Team 2018). For each sex, we ran separate models that included the focal phenotype, the mean neighborhood phenotype, and the interaction between the two as predictor variables (Figure 2). Main effects were interpreted without the interaction in the model, allowing us to examine individual and neighborhood level effects separately. This provided a picture of the overall effects of the local social environment on EPP and cuckoldry, regardless of the focal individual's phenotype. Including the interaction between focal phenotype and neighborhood mean allowed us to explore whether the local social environment

differentially affected focal individuals possessing different phenotypes. We ran models for males and females separately due to nonindependence between pair-members (same location, breeding attempt, etc.) which is also in line with previous findings within this system that individual level traits (e.g. personality) can be considered separately between the sexes (Patrick et al. 2012; Johnson et al. 2017; Firth et al. 2018). We also ran separate analyses for age and personality, because including both phenotypic traits in a common model would have reduced our sample size considerably as a fair number of birds with known ages were not assayed for personality (24% of males and ca. 22% of females). All predictors were z-transformed prior to analysis. For each model, we also included individual, year, and nestbox as random effects. Furthermore, because age and exploration behavior were not available for the entire population, models were weighted based on the proportion of neighbors in each neighborhood with known phenotypes (age for age-based models and exploration behavior for personality-based models). For example, a weight of 1 would indicate that all specified neighbors of a focal pair had a known phenotype, while a weight of 0 would indicate that none of the focal pair's neighbors had a known phenotype. Weighting our models enabled us to give due importance to group phenotypic compositions that were calculated based on a higher proportion of neighbors with known phenotypes (i.e. high confidence measurements) and the appropriate amount of importance assigned to group phenotypic compositions that were calculated based on lower proportions of neighbors with known phenotypes (i.e. low confidence measurements) when estimating model parameters (Carroll and Ruppert 1988; Ryan 1997.). This helped us account for missing data. Missing ages in our dataset resulted from individuals whose identities were unknown (often due to nests failing before parents could be identified), while missing exploration behavior scores could be attributed to either unknown individuals or birds with known identities who had not been assayed for exploration behavior.

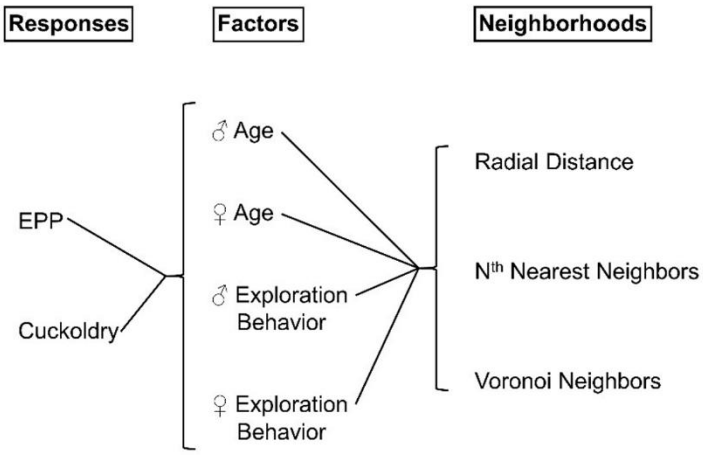

Figure 2. Diagram of the generalized linear mixed models used to test for the effects of neighborhood age and exploration behavior composition on EPP and cuckoldry. For each definition of neighborhood, we examined: 1) a model containing the focal phenotype and the neighborhood phenotypic mean, and 2) a model containing the focal phenotype, neighborhood phenotypic mean, and the interaction between the two. In total 48 models were tested. For each model, individual, year, and nestbox were entered as random effects. Models were weighted by the proportion of neighbors with known phenotypes.

Spatial Autocorrelation

Because our analyses assumed data points were independent of one another, we needed to assess whether spatial autocorrelation was present in our data, as it is appropriate correct for strong spatial autocorrelation. In other words, we examined whether any of our response or predictor variables had a propensity to aggregate spatially. We tested for spatial autocorrelation in our response variables and predictors within each year using Moran's Indices. We calculated Moran's Indices for each of the variables using the ape package and found no evidence of spatial autocorrelation, regardless of which definition of neighborhood we used (Table S1). The lack of spatial autocorrelation in our data suggested that our measured outcomes were independent of one another, allowing us to use generalized linear mixed models to analyze our data, without correcting for spatial autocorrelation.

Results

Summary

A total of 315 broods were observed in this study (117 in 2005, 92 in 2006, and 106 in 2007), of these, 160 were genotyped. Cuckoldry occurred in 98 of the genotyped broods (31%; 29 broods in 2005, 34 broods in 2006, and 35 broods in 2007). Across years, 64%-69% of males and 66%-77% of females had been aged respectively; 39%-51% of males and 45%-65% of females had been assayed for exploration behavior respectively (Table S2).

Based on frequency distributions of EPP events (see Methods) our three definitions of neighborhood were: 1) all breeding pairs within a 400 m radius (Radial Distance), 2) all breeding pairs within 25 nearest neighbors (Nearest Neighbors), and 3) all breeding pairs within four Voronoi neighbors (i.e. within four breeding territories away from the focal nest; Voronoi Neighbors; see Figures 1b and S1). At each of these three measures of distance, the frequency of EPP became low on the distribution of EPP frequency against the distance of the EPP event (Figure 1b), and the probability of EPP was extremely unlikely (i.e. below 1%; Figure S1).

Across neighborhood definitions, the proportion of male neighbors with known ages ranged from 0.389 – 0.909 (Radial distance mean = 0.642 ± 0.086; Nearest neighbors mean = 0.638 ± 0.120; Voronoi neighbors mean = 0.654 ± 0.101) and the proportion of female neighbors with known ages ranged from 0.440 - 1.000 (Radial distance mean = 0.728 ± 0.089; Nearest neighbors mean = 0.719 ± 0.112; Voronoi neighbors mean = 0.734 ± 0.100; see Weights column in Tables 1 and 2). The proportion of male neighbors with known exploration behavior scores ranged from 0.091 – 0.773 (Radial distance mean = 0.481 ± 0.110; Nearest neighbors mean = 0.486 ± 0.150; Voronoi neighbors mean = 0.482 ± 0.124) and the proportion of female neighbors with known exploration behavior scores ranged from 0.240 - 1.000 (Radial distance mean = 0.567 ± 0.129; Nearest neighbors mean = 0.562 ± 0.149; Voronoi neighbors mean = 0.564 ± 0.142; see Weights column in Tables 3 and 4). Pearson's product-moment correlations suggested that neighborhood means were positively correlated, with varying strength, across neighborhood definitions for male age (between radial distance and

nearest neighbors: r = 0.171, p = 0.037, N = 150; between radial distance and Voronoi neighbors: r = 0.538, p < 0.001, N = 150; between nearest neighbors and Voronoi neighbors: r = 0.294, p < 0.001, N = 150), female age (between radial distance and nearest neighbors: r = 0.539, p < 0.001, N = 147; between radial distance and Voronoi neighbors: r = 0.599, p < 0.001, N = 147; between nearest neighbors and Voronoi neighbors: r = 0.496, p < 0.001, N = 147), male exploration behavior (between radial distance and nearest neighbors: r = 0.666, p < 0.001, N = 114; between radial distance and Voronoi neighbors: r = 0.655, p < 0.001, N = 114; between nearest neighbors and Voronoi neighbors: r = 0.628, p < 0.001, N = 114), and female exploration behavior (between radial distance and nearest neighbors: r = 0.788, p < 0.001, N = 115; between radial distance and Voronoi neighbors: r = 0.849, p < 0.001, N = 115; between nearest neighbors and Voronoi neighbors: r = 0.808, p < 0.001, N = 115). Furthermore, a Pearson's product-moment correlation yielded a moderate positive assortment for age between males and females of a breeding pair ($r = 0.287$, $p < 0.001$, $N = 196$) but no assortment for exploration behavior ($r = -0.099$, $p = 0.297$, $N = 113$).

Table 1. The effects of focal age, mean neighborhood age, and the interaction between focal and mean neighborhood age on EPP gained by the focal male.

Predictor	Est. ± SE	*Z*	*P*	N	Weights
Male Age					
Radial Distance				150	0.423 - 0.833
Focal	0.383 ± 0.228	1.677	0.093		
Mean neighborhood	-0.163 ± 0.248	-0.656	0.512		
Interaction	0.050 ± 0.218	0.231	0.817		
Nearest Neighbor				150	0.389 - 0.880
Focal	0.484 ± 0.252	1.921	0.055		
Mean neighborhood	0.297 ± 0.264	1.123	0.261		
Interaction	-0.422 ± 0.346	-1.220	0.222		
Voronoi Neighbors				150	0.393 - 0.909
Focal	0.347 ± 0.228	1.524	0.127		
Mean neighborhood	-0.372 ± 0.249	-1.492	0.136		
Interaction	-0.036 ± 0.243	-0.148	0.883		
Female Age					
Radial Distance				147	0.536 - 0.929
Focal*	0.503 ± 0.215	2.340	0.019		
Mean neighborhood	0.152 ± 0.228	0.665	0.506		
Interaction	0.084 ± 0.176	0.479	0.632		
Nearest Neighbors				147	0.440 - 0.920
Focal*	0.518 ± 0.218	2.382	0.017		
Mean neighborhood	0.332 ± 0.239	1.391	0.164		
Interaction	-0.062 ± 0.232	-0.269	0.788		
Voronoi Neighbors				147	0.529 - 1.000
Focal*	0.467 ± 0.213	2.189	0.029		
Mean neighborhood	0.038 ± 0.218	0.175	0.861		
Interaction	0.097 ± 0.241	0.403	0.687		

*Indicates a significant effect, for details see Results: Extrapair Paternity Gained.

The outputs for focal age and mean neighborhood age are reported for the models containing main effects only, whereas the outputs for the interaction between focal and mean neighborhood age are reported for the models containing both main effects and the interaction between them. The "Weights" column represents the proportion of neighbors with known phenotypes for each model. We weighted models by this value so neighborhood averages that were calculated based on less complete records had less influence over model outcomes.

Table 2. The effects of focal age, mean neighborhood age, and the interaction between focal and mean neighborhood age on cuckoldry at the focal nest.

Predictor	Est. ± SE	*Z*	*P*	N	Weights
Male Age					
Radial Distance				150	0.423 - 0.833
Focal	0.161 ± 0.227	0.710	0.478		
Mean neighborhood	0.145 ± 0.230	0.631	0.528		
Interaction	-0.121 ± 0.224	-0.542	0.588		
Nearest Neighbors				150	0.389 - 0.880
Focal	0.098 ± 0.244	0.402	0.687		
Mean neighborhood	0.234 ± 0.251	0.932	0.351		
Interaction	0.380 ± 0.327	1.164	0.245		
Voronoi Neighbors				150	0.393 - 0.909
Focal	0.060 ± 0.227	0.263	0.792		
Mean neighborhood	-0.248 ± 0.225	-1.098	0.272		
Interaction	-0.071 ± 0.229	-0.310	0.757		
Female Age					
Radial Distance				147	0.536 - 0.929
Focal	0.042 ± 0.204	0.208	0.836		
Mean neighborhood	0.026 ± 0.206	0.127	0.899		
Interaction	-0.130 ± 0.194	-0.667	0.505		
Nearest Neighbors				147	0.440 - 0.920
Focal	0.075 ± 0.207	0.362	0.718		
Mean neighborhood	0.171 ± 0.213	0.803	0.422		
Interaction	-0.056 ± 0.223	-0.249	0.803		
Voronoi Neighbors				147	0.529 - 1.000
Focal	0.034 ± 0.204	0.164	0.870		
Mean neighborhood	0.003 ± 0.201	0.014	0.989		
Interaction	-0.149 ± 0.243	-0.612	0.540		

The outputs for focal age and mean neighborhood age are reported for the models containing main effects only, whereas the outputs for the interaction between focal and mean neighborhood age are reported for the models containing both main effects and the interaction between them. The "Weights" column represents the proportion of neighbors with known phenotypes for each model. We weighted models by this value so neighborhood averages that were calculated based on less complete records had less influence over model outcomes.

Table 3. The effects of focal exploration behavior, mean neighborhood exploration behavior, and the interaction between focal and mean neighborhood exploration behavior on EPP gained by the focal male.

Predictor	Est. ± SE	*Z*	*P*	N	Weights
Male Exploration Behavior					
Radial Distance				114	0.147 - 0.679
Focal	0.477 ± 0.395	1.208	0.227		
Mean neighborhood	0.074 ± 0.413	0.180	0.857		
Interaction	0.498 ± 0.544	0.915	0.360		
Nearest Neighbors				114	0.091 - 0.720
Focal	0.178 ± 0.370	0.480	0.631		
Mean neighborhood	0.123 ± 0.443	0.278	0.781		
Interaction	0.707 ± 0.542	1.306	0.192		
Voronoi Neighbors				114	0.129 - 0.773
Focal	0.439 ± 0.386	1.136	0.256		
Mean neighborhood	-0.152 ± 0.430	-0.355	0.723		
Interaction	0.902 ± 0.567	1.591	0.112		
Female Exploration Behavior					
Radial Distance				115	0.289 - 0.875
Focal	0.561 ± 0.323	1.734	0.083		
Mean neighborhood	-0.085 ± 0.300	-0.283	0.777		
Interaction	-0.434 ± 0.321	-1.354	0.176		
Nearest Neighbors				115	0.240 - 0.880
Focal	0.445 ± 0.313	1.424	0.154		
Mean neighborhood	-0.124 ± 0.297	-0.416	0.678		
Interaction	-0.467 ± 0.335	-1.395	0.163		
Voronoi Neighbors				115	0.267 - 1.000
Focal	0.567 ± 0.330	1.719	0.086		
Mean neighborhood	-0.151 ± 0.302	-0.501	0.616		
Interaction	-0.436 ± 0.336	-1.297	0.195		

The outputs for focal exploration behavior and mean neighborhood exploration behavior are reported for the models containing main effects only, whereas the outputs for the interaction between focal and mean neighborhood exploration behavior are reported for the models containing both main effects and the interaction between them. The "Weights" column represents the proportion of neighbors with known phenotypes for each model. We weighted models by this value so neighborhood averages that were calculated based on less complete records had less influence over model outcomes.

Table 4. The effects of focal exploration behavior, mean neighborhood exploration behavior, and the interaction between focal and mean neighborhood exploration behavior on cuckoldry at the focal nest.

Predictor	Est. ± SE	*Z*	*P*	N	Weights
Male Exploration Behavior					
Radial Distance				114	0.147 - 0.679
Focal	0.172 ± 0.366	0.468	0.640		
Mean neighborhood	-0.119 ± 0.392	-0.303	0.762		
Interaction	-0.225 ± 0.430	-0.525	0.600		
Nearest Neighbors				114	0.091 - 0.720
Focal	0.025 ± 0.337	0.075	0.940		
Mean neighborhood	-0.024 ± 0.406	-0.058	0.954		
Interaction	-0.100 ± 0.419	-0.239	0.811		
Voronoi Neighbors				114	0.129 - 0.773
Focal	0.123 ± 0.363	0.338	0.735		
Mean neighborhood	-0.127 ± 0.401	-0.316	0.752		
Interaction	0.102 ± 0.447	0.227	0.820		
Female Exploration Behavior					
Radial Distance				115	0.289 - 0.875
Focal	0.076 ± 0.267	0.286	0.775		
Mean neighborhood	-0.210 ± 0.258	-0.815	0.415		
Interaction	-0.079 ± 0.242	-0.326	0.744		
Nearest Neighbors				115	0.240 - 0.880
Focal	0.008 ± 0.273	0.030	0.976		
Mean neighborhood	-0.090 ± 0.270	-0.335	0.738		
Interaction	-0.056 ± 0.256	-0.218	0.827		
Voronoi Neighbors				115	0.267 - 1.000
Focal	0.085 ± 0.273	0.310	0.757		
Mean neighborhood	-0.062 ± 0.259	-0.241	0.810		
Interaction	-0.039 ± 0.249	-0.156	0.876		

The outputs for focal exploration behavior and mean neighborhood exploration behavior are reported for the models containing main effects only, whereas the outputs for the interaction between focal and mean neighborhood exploration behavior are reported for the models containing both main effects and the interaction between them. The "Weights" column represents the proportion of neighbors with known phenotypes for each model. We weighted models by this value so neighborhood averages that were calculated based on less complete records had less influence over model outcomes.

Extrapair Paternity Gained

For models containing focal phenotype and neighborhood phenotypic mean only, we found that focal female age was a significant predictor of whether her social mate gained EPP. Males paired with older females were more likely to sire extrapair young. This relationship was consistent regardless of which neighborhood variable was present in the generalized linear mixed model (with a binomial family and scaled response variables; model with radial distance: Est. ± SE = 0.500 ± 0.217, $Z = 2.305$, $p = 0.021$, $N = 160$; model with nearest neighbors: Est. ± SE = 0.481 ± 0.216, $Z = 2.228$, $p = 0.026$, $N = 160$; model with Voronoi neighbors: Est. ± SE = 0.459 ± 0.215, $Z = 2.135$, $p = 0.033$, $N =$

160; Figure 3; Table 1). We did not detect an effect of focal male age or focal male or female exploration behavior on EPP (Tables 1 and 3). Furthermore, across all three definitions of neighborhood, mean neighborhood age or exploration behavior did not predict EPP, for either male or female neighborhood means. For models examining the interaction between focal phenotype and neighborhood phenotypic mean, we did not detect any interaction effects for male age, female age, male exploration behavior, or female exploration behavior, regardless of how we defined neighborhood (Tables 1 and 3).

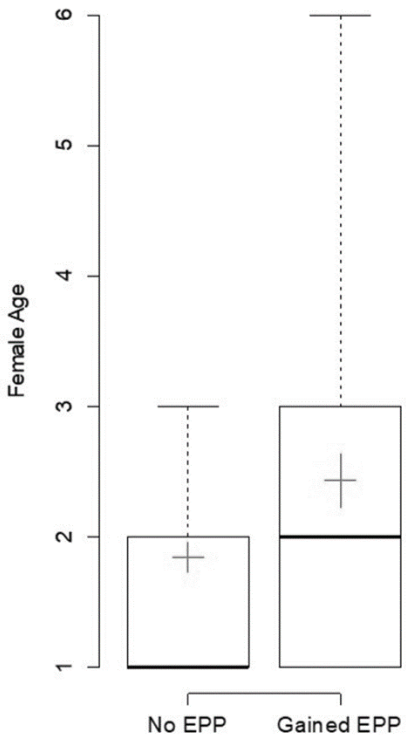

Figure 3. Summary of the raw data in relation to whether or not a male gained EPP and the age of his female social partner. Males who gained EPP (N=46) were paired to older females than males who had no observed occurrences of gaining EPP (N=123). This relationship held regardless of how mean female neighborhood age was defined in the model (see Table 1). The boxes show the interquartile range, thick horizontal mid lines show the median, and the whiskers show the range (with values outside 1.5x the interquartile range excluded). The crosses show the mean and associated standard error.

Cuckoldry

For models containing focal phenotype and neighborhood phenotypic mean only, we did not detect an effect of focal age or exploration behavior on cuckoldry within the focal nest, regardless of whether we examined male or female phenotype, and regardless of how we defined a neighborhood (Tables 2 and 4). Similarly, when we examined the interaction between focal phenotype and neighborhood phenotypic mean, there was no evidence of an interaction between the main effects, for any definition of neighborhood, for male age, female age, male exploration behavior, or female exploration behavior (Tables 2 and 4).

Discussion

Using an extensive dataset describing realized paternity between individuals of known phenotypes within a wild bird population, we conducted an exploratory analysis examining the links between extrapair paternity (EPP) and cuckoldry and the focal individual's phenotype and the local social environment. Furthermore, we explored whether the local social environment had differential effects on EPP and cuckoldry depending on the focal individual's phenotype. Overall, we found no evidence of neighborhood effects, and little evidence of individual effects, on EPP and cuckoldry, only finding a relationship between female age and the EPP gained by her social mate. This was consistent across three definitions of neighborhood.

We found that the probability of EPP or cuckoldry decreased with increasing distance between focal and neighboring nests. This pattern may occur simply as a result of practical constraints (i.e. closer neighbors are easier to travel to). However, possible alternative explanations for the observed pattern also exist. First, both males and females may be better able to assess the quality of potential mates when they are in closer proximity to the focal individual's own nest. Thus, a preference may arise for closer extrapair mates. Second, females may be more likely to gain direct benefits (e.g. males allowing territory intrusions) from extrapair males whose nests are closer to their own. Our results parallel spatial distributions of EPP events demonstrated in other species, including blue tits

(Kempenaers et al. 1997; Schlicht et al. 2015), common yellowthroats (*Geothlypis trichas*; Taff et al. 2013), northern house wrens (*Troglodytes aedon aedon*; LaBarbera et al. 2010), and southern house wrens (*Troglodytes aedon bonariae*; LaBarbera et al. 2010).

In great tits, older males have been shown to sire more extrapair young (Araya-Ajoy et al. 2016; but see Abbey-Lee et al. 2018). Furthermore, some past work has demonstrated that yearling males may be more likely than older males to be cuckolded and have a higher proportion of extrapair young in their nests (Lubjuhn et al. 2007), while other studies have shown no effect of male age on cuckoldry (Araya-Ajoy et al. 2016). Moreover, previous work has shown that individual males experience a decrease in the proportion of extrapair young in their nests as they age (Lubjuhn et al. 2007). Although past studies have found no direct effect of female age on cuckoldry in great tits (Lubjuhn et al. 2007; Abbey-Lee et al. 2018), Lubjuhn et al. (2007) found a marginally non-significant trend that yearling males paired with females aged 3 or older possessed broods containing relatively higher proportions of extrapair young. Additionally, when two individuals were excluded from the analysis, Lubjuhn et al. (2007) found that across years, there was a significant decrease in the proportion of extrapair young within an individual female's brood as she aged.

Although we did not detect an effect of focal male age, mean neighborhood male age, or the interaction between the two, we found that focal female age influenced EPP. Males paired with older females were more likely to sire extrapair young. This effect may be caused by males using EPP as infertility insurance when paired with an older female. EPP has been proposed as a method of infertility insurance against sterile males, however, female infertility or reproductive decline has received less attention. Reproductive senescence is known to occur in female great tits (Holmes et al. 2003; Bouwhuis et al. 2009). After the age of 2.8, reproductive senescence has been shown to affect 21% of great tit females annually, reducing brood size and fledgling number in older females (Bouwhuis et al. 2009). Males paired with older females may thus have higher motivation to seek extrapair copulations than males paired with younger social mates. It is also possible that older females may induce higher rates of within pair copulation behavior in males, which may cause males

socially paired with older females to invest more in behaviors related to fertilization than males paired with younger females. An increased investment in such behaviors may "spillover" to affect extrapair copulatory behavior, thus increasing the likelihood of EPP for males paired with older social mates (Araya-Ajoy et al. 2015). Furthermore, the positive relationship between male age and EPP in our study was marginally non-significant across neighborhood definitions. However, because we found moderate assortative mating with respect to age, and because older females were more likely to have partners who gained EPP, it may be the case that any estimate of the effect of male age on the siring of extrapair young is actually influenced by this age-assortative mating.

In general, carrying out multiple variations of models of a similar structure (and assessing a similar underlying hypothesis) can have positive implications (e.g. allowing sensitivity analysis, providing more details of specific patterns, etc.) and negative implications (e.g. multiple testing, altering the interpretation of individual significance levels, etc.), both of which should be considered when interpreting model outputs and drawing biologically relevant conclusions. As such, in this case, it is important to consider that the effect of female age was found consistently across multiple definitions of neighborhood types (i.e. it was not sensitive to variations in this spatial aspect) but also that the significance levels were sometimes moderate (despite always being < 0.05). More generally, it should also be considered that, across the entirety of the analysis, a total of 48 models were run, providing sensitivity analysis but also potentially changing the interpretation of each individual finding (i.e. conclusions about effects should be drawn from across the models, rather than from individual models irrespective of the other reported results).

Interestingly, we did not detect an effect of female neighborhood age composition on EPP. This pattern was consistent, whether we defined a neighborhood using a measure of radial distance, nearest neighbors, or Voronoi neighbors. We might expect males paired with older females and surrounded by younger females to be most likely to gain EPP, as younger females should provide better infertility insurance. As such, if a male seeks extrapair copulations as insurance against a potentially infertile social mate, it may seem more beneficial to copulate with younger extrapair

females, as older extrapair mates may also be at risk for reproductive senescence. However, our results suggested no such pattern.

We also did not detect an effect of focal male or female exploration behavior on EPP or cuckoldry at the individual level, neighborhood level, or interaction between the two. A previous study on our population, which aimed to investigate the interactive effects of pairs' personalities, specifically for nests in which both parents were known, found that, compared to slower exploring males, faster explorers sired more extrapair young and gained a higher proportion of their total paternity via extrapair young (Patrick et al. 2012). Slower exploring males were, however, shown to sire more within pair young than faster exploring males (Patrick et al., 2012). Although, similar to our results, male exploration behavior was found to have no effect on the occurrence of EPP or cuckoldry, Patrick et al. (2012) found that males with faster exploring social mates were more likely to gain EPP. In light of this previous study, whilst a raw overall relationship between female exploration behavior and the occurrence of EPP may exist, we found that this was ameliorated when considering not just the overall effect, but also the effect of mean neighborhood exploration behavior. Our study supports other previous work finding no specific effect of female exploration behavior on mating behavior in our population (Johnson et al. 2017; Firth et al. 2018). Furthermore, in contrast to Patrick et al.'s (2012) findings, in a German population of great tits, Araya-Ajoy et al. (2016) found that, on average, males gained less EPP across years when they were shown to be faster exploring, on average, over multiple years. In this same population, faster exploring males may also mate with fewer extrapair partners than slower exploring males (Abbey-Lee et al. 2018).

In our dataset, only a proportion of the birds in each neighborhood had known ages or exploration behavior scores. We attempted to deal with this challenge by weighting our data by the proportion of birds with known phenotypes, so that less importance was given to neighborhood averages that were calculated based on less complete records. Missing data is a common issue for behavioral studies in wild populations. Indeed, it is possible that the lack of statistically significant patterns within our results, for any of our measures of group phenotypic composition, may be partly

due to incomplete datasets. This is especially true for exploration behavior, where there was 49% - 61% of male neighbors with unknown exploration behavior and 35% - 55% of female neighbors with unknown exploration behavior, across years. However, these proportions of individuals with known personalities still represents a significant step forward in assessing such patterns in the wild. Furthermore, it is possible that catching biases may have been generated by age (e.g. Pienkowski and Dick 1976; Insley and Etheridge 1997) or personality (e.g. Carter et al. 2012; Garamszegi et al. 2009; but see Michelangeli et al. 2015). Such biases would have caused unknown individuals to be a non-representative sample of the population. We ring locally born birds while they are nestlings, thus, this should reduce sampling bias with respect to age, as all such biases could only be generated by differential trapping of immigrants. Exploration behavior, on the other hand, has a larger potential to skew our dataset, given that adult or juvenile birds must be trapped before personality assays can be conducted. We attempted to minimize catching biases by utilizing two trapping methods (i.e. mist netting and roost box checks), but this may not have eliminated all bias.

In conclusion, we find that partner age, rather than neighborhood effects, affect EPP in a socially monogamous passerine. Our study was unique in that it tested discrete phenotypic traits, which can be measured at the level of the individual. We show that focal female age affects the acquisition of EPP by her social mate. Further studies across various systems are now needed to assess the extent to which group phenotypic composition affects fitness in the wild. Such work will elucidate the potential for the distribution of individual age or personality phenotypes to affect the operation of social selection and the consequences for the evolutionary trajectories of these traits.

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Data Accessibility Statement

Analyses reported in this article can be reproduced using the data deposited in Dryad.

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Supplementary Information

Patrick et al. (2012) found that using a MasterBayes model based on genotypic and phenotypic data (MbGP_Wang) assigned more fathers with both 80% and 95% confidence than a MasterBayes model based solely on genetic data (MbG_Wang). Despite this, we used MbG_Wang for a couple of reasons. First, because the Euclidean distance between potential fathers' nextboxes and the nestboxes of DNA sampled chicks is used to calculate paternity under MbGP_Wang, using both genetic and phenotypic data would have biased how we defined neighbors (see Methods: Statistical Methods). Second, Patrick et al. (2012) found that MbGP_Wang only increased the paternity assignment by ca. 10% (MbG_Wang assigned ca. 80% of chicks' fathers with 80% assignment confidence while MbGP_Wang assigned ca. 90% of chicks' fathers with 80% assignment confidence). Given that paternity assignment was still high under MbG_Wang, we considered this method to be an acceptable way to assign paternity.

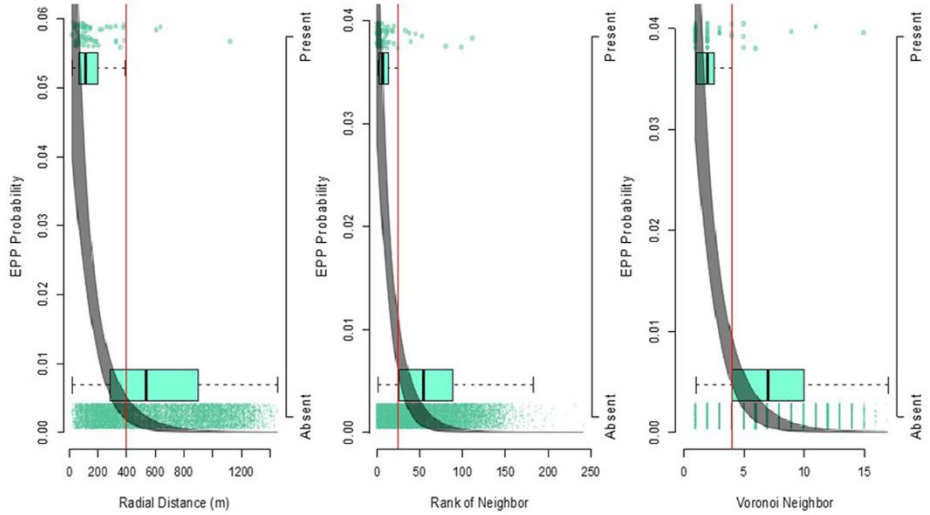

Figure S1. EPP events in nests with genotyped chicks and the (a) radial distance, (b) ranked distance and (c) Voronoi neighbor order of other nests with genotyped fathers (x-axis). Black shaded lines show the 95% probability estimate from a binomial GLMM (left y-axis) and the points show the raw data of EPP (presence vs. absence - right y-axis). The boxplots summarize the distribution of these points, with mid-lines denoting the median, boxes showing the interquartile range, and whiskers indicating the range (with values outside 1.5 times the interquartile range excluded). As in Figure 1b in the main text, the vertical lines indicate the cut-offs used when considering the potential surrounding social environment in relation to potential EPP events in further analysis.

Table S1. Observed Moran's Indices (Moran's I).

	2005 Moran's I	2006 Moran's I	2007 Moran's I
EPP			
Radial Distance	0.008	-0.050	-0.008
Nearest Neighbors	0.022	-0.071	0.039
Voronoi Neighbors	-0.001	0.028	-0.031
♂ **Age**			
Radial Distance	-0.034	-0.041	-0.022
Nearest Neighbors	-0.035	-0.014	-0.056
Voronoi Neighbors	-0.046	-0.023	-0.009
♀ **Age**			
Radial Distance	-0.030	-0.007	-0.015
Nearest Neighbors	-0.030	0.012	-0.031
Voronoi Neighbors	-0.018	0.004	-0.017
♂ **Exploration Behavior**			
Radial Distance	-0.051	-0.050	-0.051
Nearest Neighbors	-0.053	-0.050	-0.016
Voronoi Neighbors	-0.091	-0.043	0.005
♀ **Exploration Behavior**			
Radial Distance	-0.061	-0.032	-0.012
Nearest Neighbors	-0.009	-0.022	-0.014
Voronoi Neighbors	-0.032	-0.002	0.013

There was no significant difference between the observed and expected Moran's Is for any of the tested variables, suggesting a lack of spatial autocorrelation.

Table S2. Percentage of individuals with known ages and exploration behaviors for each study year.

	N_{Known}	$N_{Unknown}$	% Known
♂ **Age**			
2005	75	42	64.1%
2006	63	29	68.5%
2007	69	37	65.1%
♀ **Age**			
2005	77	40	65.8%
2006	71	21	76.3%
2007	82	24	77.4%
♂ **Exploration Behavior**			
2005	45	72	38.5%
2006	47	45	51.1%
2007	51	55	48.1%
♀ **Exploration Behavior**			
2005	53	64	45.3%
2006	52	40	56.5%
2007	69	37	65.1%

Chapter 3

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

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

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Abstract

The evolutionary significance of animal personalities (consistent interindividual behavioral differences) remains little understood. Here, we present a comprehensive investigation of the hypothesis that personality plays a role in sexual selection. We examined how two repeatable behaviors – exploration and boldness – are associated with pre- and postcopulatory sexual selection in male red junglefowl, *Gallus gallus*, using replicate groups across three sex ratio treatments. In female-biased groups, very fast- and very slow-exploring males experienced the highest mating success and lowest sperm competition intensity. Across all sex ratios, very fast- and very slow-exploring males harassed females proportionally less, and faster-exploring males associated with females more and received more sexual solicitations. 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 faster-exploring males decreased with the proportion of faster-exploring males in a group, consistent with negative frequency dependent sexual selection. Boldness did not predict mating performance, however, there was a tendency for males and females to mate disassortatively with respect to boldness. Collectively, our results indicate that sexual selection on personality is contingent

on the social environment, and often subtle, and reveal that group-level mechanisms may help maintain personality variation.

Keywords: boldness, exploration, disassortative mating, negative frequency dependence, group-level selection

Introduction

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

Sexual selection arises from differential reproductive success among members of the same sex, caused by intrasexual competition over access to reproductive partners and their gametes (Darwin, 1871; Andersson, 1994). In males, where intrasexual competition is typically more intense (Bateman, 1948; Kokko et al., 2006), variation in reproductive success is governed by precopulatory mechanisms

determining the number of females mated (i.e. mating success) and, in species where females mate with multiple males (polyandry), by postcopulatory mechanisms affecting the proportion of available eggs that a male's sperm fertilize by outcompeting the sperm of other males (i.e. paternity share; Parker, 1970; Parker and Birkhead, 2013; Firman et al., 2017). Sexual selection may favor males with personality types associated with certain behaviors or physiological responses (Verbeek et al., 1999; Cockrem, 2007; Reaney & Backwell, 2007) if, for example, these behaviors influence a male's access to mates via intrasexual selection (Schuett et al., 2010). In rainbow fish, *Melanotaenia duboulayi*, bolder, more active, and more aggressive males achieve a higher dominance rank, which confers a reproductive advantage in this species (Colléter & Brown, 2011). Personality may also influence a male's reproductive success via intersexual selection (Godin & Dugatkin, 1996; Reaney & Backwell, 2007; Schuett et al., 2010; 2011; Dzieweczynski et al., 2013; Teyssier et al., 2014). For example, in fiddler crabs, *Uca mjoebergi*, females were shown to prefer bolder males, and these males spent more time courting females, and obtained more mates (Reaney & Backwell, 2007). Furthermore, the evolution of female preferences for male personalities could, in principle, be explained if personality-related behaviors are costly, making male personality an indicator of a male's breeding value for viability and/or parental ability (Schuett et al., 2010; Tuni et al., 2018). For example, the energetic costs of faster-exploring or bolder individuals may exceed those of slower-exploring or shyer individuals (Biro & Stamps, 2010; although, in certain species or environments, the costs of higher metabolic rates may be outweighed by higher encounter rates with food for faster exploring and bolder individuals, leading to net energy gains instead of costs; Mathot & Dingemanse, 2015; Mathot et al., 2019). Similarly, bolder or faster-exploring individuals may face more risks than shyer or slower-exploring individuals (reviewed in Schuett et al., 2010). Female personality may play a key role in sexual selection on male personality, by influencing criteria of female preference, female choosiness, and female preference functions. An interaction between male and female personality may also influence a male's mating performance if, for example, females prefer males that are behaviorally similar to themselves, leading to assortative mating (Schuett et al., 2010; Montiglio et al., 2016). To

illustrate this point, moderately and faster-exploring female zebra finches, *Taeniopygia guttata*, have been shown to prefer exploratory males compared to unexploratory males, whereas females with slower exploratory tendencies exhibit no preference for male exploration (Schuett et al., 2011). Choosing a behaviorally similar mate may confer advantages, as similar pairs may be better able to coordinate activities such as food provisioning and nest defense (Schuett et al., 2010). Alternatively, females may prefer mates that are behaviorally dissimilar to themselves, promoting disassortative mating (Dingemanse et al., 2004; Both et al., 2005; van Oers et al., 2008; Montiglio et al., 2016). Such pairings may confer advantages if intermediate offspring are more viable than extreme offspring or if assortative pairs are genetically or behaviorally incompatible (Dingemanse et al., 2004; Schuett et al., 2010).

In polyandrous species, personality may also influence postcopulatory sexual selection on males. Male personality, female personality, or their interaction could influence 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 a male mates with a female. 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). In the more promiscuous field cricket, *Gryllus bimaculatus*, on the other hand, male aggression has been shown to be positively correlated (at both genetic and phenotypic level) with ejaculate size, a measure of investment in sperm competition, suggesting that–all else being equal–consistently more aggressive males may be favored 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 the social environment. First, the sex ratio of groups is predicted to influence the intensity and mechanisms of pre- and postcopulatory sexual selection (Emlen & Oring, 1977; Bleu et al., 2012; Kvarnemo & Simmons, 2013; but see Pröhl, 2002; Wey et al., 2015) and the relationship between pre- and postcopulatory competition (Wey et al., 2015). Group sex ratio could therefore play an important role in determining the relationship between male personality and male reproductive

success by modulating selection pressures (Pröhl, 2002; Weir et al., 2011; Del Giudice, 2012; Wey et al., 2015). Second, group phenotypic composition may also have critical repercussions on patterns of selection on social behavior. Group phenotypic composition refers to any descriptor of a group's phenotypic makeup such as the mean, variance, or presence of a given phenotype (Pruitt & Ferrari, 2011; Pruitt & Riechert, 2011), and several studies have demonstrated a link between individual fitness and group personality composition (Sih & Watters, 2005; Pruitt & Ferrari, 2011; Pruitt & Riechert, 2011; Sih et al., 2014; Wey et al., 2015, but see Roth et al., in press). For example, in male water striders, *Aquarius remigis*, the presence of hyper-aggressive males in a group has been shown to depress individual-level male mating performance (i.e. number of mates, total number of copulations, proportion of time spent mating, and average duration of copulations) but increase mating exclusivity (potentially via reduction of average polyandry), irrespective of the focal individual's phenotype (Sih et al., 2014; Wey et al., 2015). The social environment may also modulate the shape of sexual selection on personality. While in closed water strider populations, directional sexual selection for more aggressive males is observed, in inter-connected populations, where females can move away from persistent male harassment, sexual selection for male aggression has a negative quadratic shape, indicating that overly aggressive males lose out by driving potential partners away (Eldakar et al., 2009; 2010a; 2010b; 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, dissimilar in personality (i.e. negative frequency dependent selection; Dall et al., 2004) or when competitors are, on average, similar in personality (i.e. positive frequency dependent selection). Little however,,is known about the way in which pre- and postcopulatory sexual selection targets male personality at both individual and group levels.

Here, we use an experimental approach to examine the role of two behavioral 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 some populations of the closely related domestic fowl, *Gallus domesticus*, with repeatable behavior reported in several traits

including exploration, boldness, and aggression (Favati et al., 2014a; 2014b; 2016; 2017; 2018; Zidar et al., 2017; 2018). Previous studies suggest that, in fowl, exploration and some measures of boldness (i.e. neophobia, tonic immobility, and fear) are uncorrelated in adults (Favati et al., 2016; 2018). In nature, red junglefowl live in small groups and form sex-specific dominance hierarchies (Lill, 1966; Thornhill, 1988; Collias et al., 1994; Collias & Collias, 1996; Kim & Zuk, 2000; Pizzari & McDonald, 2019). Status plays an important role in mediating the outcome of intrasexual competition over resources in fowl groups, and can influence the number of mates in both males and females (Lill, 1966; Thornhill, 1988; Collias et al., 1994; Collias & Collias, 1996; Kim & Zuk, 2000; Pizzari & McDonald, 2019). In principle, male personality may affect male reproductive success indirectly, by influencing male status, or directly (i.e. independently of male status). Faster-exploring male fowl have been shown to be more likely to defeat slower-exploring males in dyadic contests, but neither exploration or boldness have been found to predict social rank in a group setting (Favati et al., 2014a; 2017). Similarly, female personality may affect polyandry indirectly through an influence on female status, or directly (i.e. independently of female status).

Sexual behavior in fowl is strongly modulated by the social environment (Pizzari & McDonald, 2019). 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. 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 favored both before and after copulation (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. All else being equal, the outcome of sperm competition for eggs, ovulated shortly after insemination, is largely determined by the relative number of sperm inseminated by competing males (Martin et al., 1974; Pizzari et al., 2008). Thus, remating frequently with the same female enables dominant, aggressive males to ensure that females store a higher number of their sperm, compared to other males.

We measured the exploration and boldness of male and female red junglefowl and studied the mating behavior of individuals of known personality in 24 replicate groups under three natural sex ratios: male-biased (9 males, 3 females), even sex ratio (6 males, 6 females), and female-biased (3 males, 9 females). We addressed the following four aims. First, we investigated patterns of precopulatory sexual selection and established the role of male personality, and of the personality composition of a male's competitors, in male mating success. Second, we examined patterns of postcopulatory sexual selection. We tested whether female personality affects the degree of polyandry and the relative importance of male personality and male competitor personality composition on the levels of sperm competition intensity suffered by individual males, as well as a male's rate of remating with individual females. Third, we considered connections between male and female personality and tested whether individuals mated assortatively with respect to personality type. Finally, we considered the behavioral mechanisms underpinning differential mating patterns by investigating the role of personality in male courting of females, time spent with females, and female solicitation of males.

The patterns explored are potentially complex, which makes it difficult to generate clear *a priori* predictions. Nevertheless, we identified a number of general scenarios and expectations for each objective summarized in Table 1. Briefly, 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 behavior 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 in favor of faster-exploring and/or bolder males, and an

assortative scenario in which females would preferentially mate with males with personalities similar 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 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 inter-sexual or between pre- and post-copulatory mechanisms may also contribute to non-linear patterns of sexual selection on male personality, particularly in groups with even sex ratios (which offer considerable opportunity for both pre- and post-copulatory sexual selection) and female-biased groups (where females have more opportunity to exercise their preference). Finally, we hypothesized that the personality composition of the male competitors in a group would influence the performance of individual males. Specifically, we considered a scenario in which all 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 and better with increasing frequency of competitors of dissimilar personality type.

Table 1. General expectations investigated for each aim of our study.

Aim 1	• Faster-exploring and/or bolder males will mate with more females. • The effect of male personality on the number of females mated may be stronger in even sex ratio and female-biased groups. • Quadratic patterns may emerge as result of antagonistic mechanisms (e.g. a phenotype may be favored in male-male competition and disfavored in female preference). • There will be a negative effect of faster-exploring and/or bolder competitors on the number of females mated with for all focal males, or there will be negative frequency dependence with respect to personality and the number of females mated with.
Aim 2	• Faster-exploring and/or bolder females will be more polyandrous. • Faster-exploring and/or bolder males will remate with females at a higher rate and experience lower levels of sperm competition. • The effect of male personality on remating rates and sperm competition intensity may be stronger in male-biased groups. • Quadratic patterns may emerge as result of antagonistic mechanisms (i.e. remating rates with the same females maximized and/or levels of sperm competition minimized for males with intermediate phenotypes). • Faster-exploring and/or bolder competitors will reduce remating rates and increase levels of sperm competition for all focal males, or there will be negative frequency dependence with respect to personality and remating rates and/or sperm competition intensity levels.
Aim 3	• Faster-exploring and/or bolder females will mate more with faster-exploring and/or bolder males and slower-exploring and/or shyer females will mate more with slower-exploring and or shyer males.
Aim 4	• Faster-exploring and/or bolder males will be preferred by females (i.e they will be solicited more). • Faster-exploring and/or bolder females will solicit more. • Faster-exploring and/or bolder males will exhibit higher proportions of waltzes to harassment. • Faster-exploring and/or bolder males will associate with females more.

Methods

Study system

We studied a captive population of red junglefowl housed in outdoor aviaries 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. In order to test the role of female behavior in sexual selection on male personality we also studied personality in 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).

Personality assays

We subjected individuals to two behavioral assays: 1) a novel arena test to investigate exploration and 2) a novel object test to investigate boldness. Exploration and boldness have been examined previously in fowl using a similar protocol and found to vary among individuals (Favati et al., 2014a; 2016; Zidar et al., 2017). Both assays were modified from the methods described in Zidar et al. (2017). Before each assay, individuals were placed in a 45.5(l) × 26.5(w) × 33.5(h)cm^3 cardboard carrying box for 5 minutes, in an effort to standardize stress responses to catching across individuals. Because assays often involved rapid movements by the test subjects, we video recorded all assays (with a Motorola Nexus 6 64GB smartphone) and used the recordings to measure behavior.

i) Novel arena assay. To investigate interindividual variation in exploration, we performed novel arena assays from March to September in 2016 and March to August in 2017. We tested individuals singly in a 4.00 × 3.25m^2 novel indoor room containing five artificial trees, 1.54m in height, to facilitate exploration (Figure S1). We divided the floor of the arena into nine rectangular subareas of equal size using beige masking tape. At the onset of each assay, we placed the focal individual in the middle quadrat to the right of the central artificial tree (Figure S1) with the lights off. Assays lasted for 30 minutes and did not begin until we had vacated the room and turned the lights on. We video-recorded assays from a one-way window and measured exploration propensity as: 1) latency to 'unfreeze' (defined as taking three consecutive steps after the room was lit) to the nearest second, 2) latency to leave the starting quadrat (defined as how many seconds it took an individual to place at least one foot outside the starting quadrat), 3) latency to visit six quadrats, 4) total number of unique quadrats visited, and 5) number of transitions between quadrats (defined as the number of times an individual moved from one quadrat to another by placing at least one foot into a neighboring quadrat).

Some individuals did not unfreeze, did not leave the starting quadrat, and/or visited fewer than six unique quadrats. When this occurred, an individual was recorded as having taken 30 minutes (i.e. the duration of the assay) to perform the task. We tested each individual in the same setup between three and four times (with the exception of four males who died of natural causes after their second replicate assay; only one of these males was used in mating group trials). We conducted assays in the morning (starting from half an hour after sunrise to three hours after sunrise) and evening (starting from three hours before sunset until sunset), which capture the peaks in daily activity (Løvlie & Pizzari, 2007). Individuals tested in the morning for the first assay were tested in the evening in the second assay and *vice versa*. Morning or evening was randomly assigned to individuals for the third and fourth assays. Assays one and two were conducted 10 days apart, prior to mating group trials (see *Mating Groups* below). Assay three was conducted after mating group trials began, ca. 3-5 months after assay two, and assay four was conducted in the beginning of the subsequent breeding season, ca. one year after assay one.

ii) Novel object assay. To investigate interindividual variation in boldness, we conducted novel object assays from April to September in 2016 and March to August in 2017. Prior to testing, we placed a taupe colored bowl with mealworms (i.e. the reward bowl) inside the birds' home pens for a minimum of 5 consecutive days before the start of the assay to familiarize birds with the reward bowl. All tested individuals fed from the reward bowl in their home pens. Following this 5-day training period, we assayed the same 94 individuals used for the novel arena assays. We conducted novel object assays in a familiar $3.08 \times 6.66 m^2$ pen with gravel substrate, divided in half on the long edge using a familiar mesh net (Figure S1). We visually isolated the pen from adjacent pens using green or blue Tarpaulin, which was also familiar to the study birds. We placed the reward bowl 50cm from one corner of the pen and angled it slightly towards the diagonal corner so that mealworms were visible to the birds upon exiting the carrier box (see below). We created marks 0.5m from the bowl, using small twigs on the ground, and beige masking tape on the pen walls. In the diagonal corner, we placed two pieces of masking tape on the pen walls, 88cm from the corner to create an imaginary starting line

from which birds were released. We placed the carrier box on this line and opened the box to allow the bird to hop out, which is when we began timing. If birds were hesitant to leave the box, we tilted the box slightly to encourage their exit.

The assay comprised of two trials, performed on the same bird across two consecutive days, one without the novel object (i.e. baseline test), to control for interindividual differences unrelated to the novel object, and one with the novel object. We tested each individual singly in the novel object pen, and for each individual, we measured (to the nearest second): 1) latency to reach 0.5m from the reward bowl, 2) latency to reach one body length from the reward bowl, and 3) latency to feed from the reward bowl, both with (novel object trial) and without (baseline trial) a novel object. In the novel object trials, we used a yellow and black toy rubber duck (10(l) × 8.5(w) × 10(h)cm^3) as the novel object and placed it 2cm to the left of the reward bowl. We allowed individuals up to 20 minutes to feed for both the novel object and baseline trials. Some individuals did not reach 0.5m of the reward bowl, within one body length of the reward bowl, and/or did not feed from the reward bowl. In these instances, we recorded an individual as taking 20 minutes to perform the task. Similar to the novel arena assay, we assayed each individual using the same protocol 3-4 times. An additional three males could only be exposed to the first two assays as they died of natural mortality before a third assay; only one of these males was included in mating groups. We started assays between 3-5.5 hours after sunrise in an attempt to ensure that all individuals would have adequate time to feed and be satiated to approximately equal degrees to avoid effects of hunger on differential motivation to approach mealworms. The order of novel object and baseline trials were randomized across individuals in the first assay to control for any biases that may have arisen due to differential acclimation to the experimental pen. The order of the novel object and baseline trials was reversed for the second assay and was again randomized for the third and fourth assays. The first and second assays were run one month apart, assay three was conducted ca. 2-4 months after assay two, and assay four was conducted at the start of the next breeding season, ca. one year after assay one.

Mating groups.

We created 24 groups comprising 12 individuals of three different sex ratios: 8 male-biased groups (9 males, 3 females), 8 even-sex ratio groups (6 males, 6 females), and 8 female-biased groups (3 males, 9 females). We studied 12 groups May-August 2016, and 12 additional groups April-July 2017. All replicate groups were housed and studied in a $11.5 \times 7.2 m^2$ outdoor pen containing both an area of natural ground cover (dirt floor, with grass and weeds, and fallen trees) and an area with gravel substrate. 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 fast- to slow-exploring within each sex ratio. For each group, we placed males in the pen at ca. 1:00 pm local time and gave them 24 hours to establish a dominance hierarchy before introducing females to the pen at ca. 1:00 pm the following day. We conducted 3-hr behavioral observations on each group, for six evenings (three hours before sunset to sunset, local time) and five mornings (sunrise to three hours 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, and passive avoidances), intrasexual fights, and heterosexual copulation attempts. We scored copulation attempts as successful or unsuccessful. Successful copulations (i.e. 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 a male for copulation when she crouched in front of him (Etches, 1996; Pizzari, 2001; Løvlie et al., 2005; Løvlie & Pizzari 2007). For all same-sex agonistic interactions and fights, 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 minutes and recorded all individuals who were within one body length apart. A total of 77 scan samples were recorded for each of 24 groups.

Statistical Methods

Measuring personality

We used R 3.3.2 for all analyses (R Core Team, 2018). We used the first axis of a Principle Component Analysis (PCA) to summarize the different behaviors recorded in each personality assay (novel arena, novel object), following previous literature (e.g. Boon et al., 2008; Quinn et al., 2009; Starling et al., 2013; Aplin et al., 2013; 2014; Patrick & Weimerskirch, 2014; Stanley et al., 2017; Firth et al., 2018; Roth et al., in press). We analyzed males and females separately. We were interested in male personality as potential target of sexual selection, and because sexual selection is exclusively concerned with intra-sexual variation, we estimated inter-individual variance in exploration among males and the way this covaried with measures of reproductive success (number of mates, remating rates, sperm competition levels) within the male population. Furthermore, we wanted to establish the role of variation in female personality in sexual selection on males (e.g. through patterns of differential remating rates and mate preference), and thus analyzed inter-individual variance in exploration among females and the way this covaried with female mating behavior. For each sex, we normalized the behavioral measures using z-transformation (i.e. subtracting the mean and dividing by the standard deviation) and ran a PCA using the 'princomp' function.

We used the five behavioral measures of the novel arena assay (see above) to capture an individual's exploration. For males, 0.716 of variance was explained by PC1, and for females, 0.822 of variance was explained by PC1. For both sexes, PC1 had non-normal, continuous distributions (Figure S2 & S3). To calculate repeatability (i.e. interclass correlation; Nakagawa et al., 2010) of PC1, we used the 'lmer' function in R to run linear mixed models with PC1 as the response, individual identity as a random effect, and age, trial number, days since March 1st, and whether it was a morning or evening trial as fixed effects. We performed non-parametric bootstrapping with 1000 bootstrap samples using the 'lmeresampler' package and the 'boot' package in R (see Appendix 1 for code). Using non-parametric bootstrapping allowed us to relax linear model assumptions (i.e. residual

normality). PC1 was highly repeatable for both males (repeatability = 0.538, 95% CI = 0.351 - 0.591) and females (repeatability = 0.479, 95% CI = 0.260 - 0.554). Given this, we used PC1 to obtain an exploration score for each individual, taking the intercept coefficient plus the parameter for each individual from a general linear model that controlled for fixed effects. (See Appendix 2 for further detail.) Exploration scores were continuous, and individuals with higher scores were considered faster-explorers as they had lower latencies, made more transitions between quadrats, and/or visited relatively more quadrats. For binary calculations, individuals with a score > 0 were considered fast-explorers and those < 0 slow-explorers. To examine sex differences in exploration, we ran generalized linear mixed models (GLMMs) for each of the five initial behavioral measures using the 'glmmTMB' package. Each behavioral measure was included in a separate model as a response variable, sex was included as a fixed effect, and individual identity, individual age, trial number, days since March 1st, and whether it was a morning or evening trial were included as random effects. We used a Poisson family with a log link for number of quadrats visited, and a zero inflated Poisson family with a log link for the other four behavioral measures. Note, however, that this approach is utilized to simply characterize potential sex-specific patterns; since male and female explorations were quantified separately, the two behaviors are not necessarily directly comparable.

We used six behavioral measures recorded in the novel object assay (1) latency to 0.5 m from the reward bowl in the novel object trial, 2) latency to one body length from the reward bowl in the novel object trial, 3) latency to feed from the reward bowl in the novel object trial, 4) difference between the novel object and baseline trials in latency to 0.5 m from the reward bowl, 5) difference between the novel object and baseline trials in latency to one body length from the reward bowl, and 6) difference between the novel object and baseline trials in latency to feed from the reward bowl) to measure an individual's boldness. Overall, 0.533 of variance was explained by PC1 for males, and 0.595 of variance was explained by PC1 for females. PC1 was non-normally distributed for both males and females (Figure S4 & S5) so we used linear mixed models with non-parametric bootstrapping to calculate repeatability. We input PC1 as the response, individual identity as a random effect, and age,

trial number, the number of days past March 1st in which the trial began (regardless of whether the novel object or baseline test came first), and whether the novel object or baseline trail came first as fixed effects. We used 1000 bootstrap samples. PC1 was weakly to moderately repeatable for both males (repeatability = 0.226, 95% CI = -0.027 - 0.246) and females (repeatability = 0.355, 95% CI = 0.050 - 0.470), although repeatability was not significant for males. We used PC1 to calculate a boldness score for each individual (see Appendix 2 for further detail). Individuals with higher scores had lower latencies in the novel object assay and were considered to be bolder. For binary calculations, we defined bold individuals as birds with score of > 0 and shy individuals as those with a score < 0. We ran GLMMs with a Poisson family and a log link to examine potential sex differences in boldness. We included each of the six initial behavioral measures in separate models as response variables. We included sex as a fixed effect, and individual identity, individual age, trial number, the number of days past March 1st in which the trial began, and whether the novel object or baseline trial came first as random effects. Because behavioral measures that involved taking the differences between latencies in the novel object and baseline tests included negative values, we transformed differences by adding a constant to bring the minimum value for each distribution to 0.

Social hierarchies

Fowl groups have sex-specific social hierarchies, and male and female status are analyzed separately in this species (Pizzari & McDonald, 2019). We therefore used all same-sex dyadic agonistic interactions, with the exception of fights that ended in a draw, to explore status. Using the number of interactions won *versus* those lost for each individual, we calculated status as normalized David's Scores (a dyadic dominance index corrected for chance; de Vries et al., 2006) using the 'steepness' package in R. We investigated the correlation between personality and status within each sex, by running separate GLMMs with a gamma family and a log link for males and females, with status as the response, exploration, boldness, and sex ratio as fixed effects. We included individual and

group identity as random effects. Because females interacted less than males, for two of 24 groups, we did not have enough information on female status to calculate female dominance hierarchies. Furthermore, because the number of available females was limited, we had to reuse female groups with the same individual makeup for a few replicates (four female groups were used twice). We, therefore, also included female group identity as a random effect (see McDonald et al., 2017 for a similar approach). As expected, sex ratio influenced status, with higher normalized David's scores arising when more competitors were present for both males and females (Table S1). We, therefore, also included all two-way interactions between main effects, to examine if sex ratio had a differential effect on the relationship between personality and status and to examine if status could be predicted by specific combinations of exploration and boldness. Because correlations between personality and status were weak (see Results below), we included both personality and status as independent effects in subsequent models.

Aim 1. Precopulatory sexual selection: Male mating success

We examined focal male personality as a predictor of male mating success (number of females mated). We first ran an inclusive zero-inflated GLMM with a Poisson family and a log link using the 'glmmTMB' package, on the data from all sex ratios combined, and included mating success as the response, and male exploration, boldness, status, and sex ratio as fixed effects. We z-transformed exploration, boldness, and normalized David's scores (i.e. status) within each of the 24 groups ((focal value-group mean)/(SD of group); see De Lisle & Svensson, 2017). We also included the squared term for exploration (herein written exploration^2) as a fixed effect, because the relationships between male exploration and response variables appeared quadratic. We calculated exploration^2 after z-transforming exploration. To test whether sex ratio influenced the relationship between focal male phenotype and mating success, we also included all two-way interactions between group sex ratio and the other fixed effects. We added male identity, group identity, and female group identity as random

effects. 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. 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 (i.e. exploration, exploration^2, and status as fixed effects and individual identity as a random effect). Random effects of group or female group identity had little effect in the inclusive model (group identity: variance ± SD = 1.289e-12 ± 1.135e-06, female group identity: variance ± SD = 6.942e-13 ± 8.332e-07) and were excluded.

Finally, we tested the effects of competitor exploration composition on the relationship between focal male exploration and mating success. We tested each sex ratio separately, given the influence of sex ratio on the effect of focal personality, using zero-inflated GLMMs with a Poisson family and a log link. For these models, we only included fixed effects related to focal phenotype that were significant in the models above (i.e. focal exploration and status). We then included mean competitor exploration, and the interaction between focal exploration and mean competitor exploration as fixed effects, and male identity as a random effect. We calculated competitor personality composition in a group in two ways: 1) mean competitor personality and 2) the proportion of competitors with a certain personality type (e.g. the proportion of fast exploring competitors). We used the two complementary definitions of competitor phenotypic composition as complementary approaches, as both have their own 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, characterizing competitor phenotypic composition as the proportion of competitors with a certain personality type requires arbitrarily binning a continuous variable into categories; nevertheless, this allowed us to test more specifically for frequency dependent selection. We z-transformed focal exploration, focal normalized David's scores (i.e. status), and mean competitor personality within each of the three sex ratios (instead of within each of the 24 groups). We first calculated mean competitor

personality based on the untransformed personality scores of competitors. When examining the proportion of fast-exploring competitors, we replaced focal personality with a binary variable (1= fast-explorers, 0 = slow-explorers). To rule out the possibility that an effect of male group personality composition could be caused by female group personality composition, we conducted a Pearson product-moment correlation to test for a relationship between mean female group personality and mean male group personality. We found no evidence of a relationship between mean female exploration and mean male exploration (r = -0.125, p = 0.562, N = 24) or between mean female boldness and mean male boldness across groups (r = 0.100, p = 0.643, N = 24).

Aim 2. Postcopulatory sexual selection

i) Polyandry. We used a zero inflated GLMM with a Poisson family and a log link to examine whether female phenotype predicted the number of males mated. As fixed effects, we included female exploration, boldness, status, sex ratio, and all two-way interactions between sex ratio and the other fixed effects. We included individual female identity, group identity, and female group identity as random effects.

ii) Sperm Competition Intensity. We estimated the sperm competition intensity (SCI) encountered by a male as the harmonic mean of his partners' mating success, defined for the *i*th male by the following equation:

$$\mathrm{SCI}_i = \frac{1}{\frac{1}{M_i}\left(\sum_j^M \frac{1}{k_j}\right)}$$

where M_i is the number of females the *i*th male mates with and k_j is the number of males mated with by the *j*th female who mated with the *i*th male (Shuster & Wade, 2003; McDonald & Pizzari, 2016). We first examined the effects of male phenotype on sperm competition intensity using the subset of all individual males who were observed mating with at least one female, and ran a GLMM inclusive of all sex ratios, with a gamma family and a log link, male exploration, exploration^2, boldness, status, and

sex ratio as fixed effects, as well as all two-way interactions between group sex ratio and the other fixed effects. We included focal individual, group, and female group identity as random effects. We then explored the effects of male phenotype on each sex ratio separately, including exploration, exploration^2, and status in our GLMMs as fixed effects and individual and group identity as random effects. Given that female group identity had no effect in the inclusive model (Variance ± SD = 0 ± 0), we did not include it as a random effect.

We also explored whether the relationship between focal exploration and sperm competition intensity was influenced by competitor exploration composition, through GLMMs with a gamma family and a log link that included focal exploration, mean competitor exploration, and their interaction as fixed effects, as described for aim 1. We included individual and group identity as random effects.

iii) Remating rates. We used a similar approach to examine whether male and female focal phenotype predicted male and female remating rates, respectively, using separate GLMMs with a gamma family and a log link. For these analyses we used only the subset of individuals who mated with one or more partners. We included focal exploration, exploration^2 (for the male, but not the female, model), boldness, and status as fixed effects. We also included sex ratio and its two-way interactions with all other fixed effects. We added focal individual, group, and female group identity as random effects.

Aim 3. Assortative or disassortative mating

We examined whether males and females with similar or dissimilar personalities 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 (i.e. the absolute value of male exploration minus female exploration). We ran separate GLMMs with a binomial family and a logit link for exploration and boldness. Models

accounted for every possible pairing of males and females, and we used whether a male and female mated as the response variable. We included the similarity in male and female personality scores as a fixed effect and group identity, male identity, and female identity as random effects. We used 1000 randomizations of mating patterns within groups to generate 1000 randomized datasets, and we ran repeated models on these randomized datasets. We held variation in male and female mating success constant in the randomizations. We then compared empirical slopes with randomized distributions.

Aim 4. Underpinning mechanisms

We investigated the scope for different behavioral mechanisms to underpin the personality-dependent mating patterns described above. We focused on female preference (measured as solicitation of mating), the relative contribution of courting (waltzing) and harassment in male approaches to females, and physical proximity between individual males and females.

i) Solicitations. We investigated whether a male's phenotype could predict the number of solicitations he received and whether a female's phenotype could predict the number of solicitations she gave. We used separate zero inflated GLMMs with a Poisson family and a log link, including the following fixed effects: focal exploration, exploration^2 (for the male, but not the female, model), boldness, status, sex ratio, and all two-way interactions between group sex ratio and the other fixed effects. Additionally, we included focal individual, group, and female group identity as random effects. Our initial models suggested that a male's exploration and status significantly influenced the number of solicitations he received, regardless of sex ratio (see Results: *Aim 4. Underpinning mechanisms*; Table 7). We, therefore, tested the effects of competitor exploration composition on the relationship between focal exploration and the number of solicitations received. We ran zero- inflated GLMMs with a Poisson family and a log link where we included male exploration, mean competitor exploration, status, and the interaction between male exploration and mean competitor exploration as fixed effects. We added male identity as a random effect. We did not include group or female group

identity as random effects given that both had little effect in the initial model exploring the relationship between focal personality and solicitations received (group identity: Variance ± SD = 4.453e-10 ± 2.110e-05, female group identity: Variance ± SD = 3.138e-11 ± 1.771e-05).

ii) Proportion of female-directed behaviors that were waltzes. We examined whether a male's phenotype could predict the proportion of his female-directed behaviors (i.e. intersexual waltzes and harassment events) that were waltzes (i.e. a measurement of the relative contribution of courting; Zuk et al., 1990; Johnsen et al., 1995). We ran a GLMM with a binomial family and a logit link. We included male exploration, exploration^2, boldness, status, and sex ratio as fixed effects, as well as all two-way interactions between group sex ratio and the other fixed effects, and focal individual, group, and female group identity as random effects. Our initial model suggested significant interactions between male boldness and sex ratio and between status and sex ratio, as well as an overall effect of exploration^2 (see Results: *Aim 4. Underpinning mechanisms*; Table 9). Given this, we included male exploration, exploration^2, boldness, and status as fixed effects when running separate models for each sex ratio, and individual, group, and female group identity as random effects.

iii) Associations. Recent work on the same population indicates that there is a positive correlation between the amount of time that a male associates with a female and the probability that they will mate (McDonald et al., under review). We calculated the number of times male "A" was seen associating (<1 body length apart) with female "A" across scan samples. We also calculated the proportion of successful copulations that male "A" obtained with female "A" out of all the successful copulations that male "A" had across all the females in the group. We ran GLMMs with a binomial family and a logit link and included the proportion of scan samples in which a pair was associated as the response variable to examine whether focal phenotype influenced how much time a male spent associating with a female. We included the proportion of successful copulations, focal male exploration, focal male boldness, focal male status, and group sex ratio as fixed effects. We included all two-way interactions between the proportion of successful copulations and the focal male's phenotype to assess whether males with certain personalities spent disproportionately more time

associating with the females with whom they mated more frequently. We incorporated male identity, female identity, group identity, and female group identity as random effects.

Results

General patterns

Basic patterns of exploration and boldness were not strongly sexually dimorphic in this population (Table S2). Given that the multivariate response to selection is likely to depend on genetic correlation structure of behavior, an important prerequisite to resolving the role of sexual selection in personality variation is to establish patterns of behavioral trait correlations in a population (Lande & Arnold, 1983; Dochtermann & Dingemanse, 2013). For each sex, we examined the relationship between an individual's exploration and boldness scores arising from PC1, using a Pearson product-moment correlation. The two behavioral traits were not inter-correlated in either sex (males: $r = 0.170$; $p = 0.209$, N=56; females: $r = 0.064$, $p = 0.704$, $N = 38$). We found a weak correlation between male boldness and male status, in that shyer males were more dominant (Table S1). In females, we found a weak correlation between exploration and status, in that slower-exploring females were more dominant (Table S1). Furthermore, when tested against the intercept, shyer females were more dominant in male-biased groups (Table S1), however, a likelihood ratio test comparing the full model with a model without the boldness×sex ratio interaction showed the interaction was not significant (Chi-squared = 4.477, df =2, p = 0.107). Group sex ratio influenced patterns of mating behavior (Table S3) in a way broadly consistent with expectations (Løvlie & Pizzari 2007; Pizzari & McDonald, 2019).

Aim 1. Precopulatory sexual selection: Male mating success

We first explored the role of focal male personality in mating success, considering all sex ratio treatments. Dominant males obtained a higher number of mates (Table 2). Sex ratio also had an effect, with males obtaining fewer mates in male-biased groups and more mates in female-biased groups

compared to even-sex ratio groups (Table 2). Importantly, there was some evidence for an interaction between exploration^2 and sex ratio. When compared to the intercept, males at both extremes of the exploration spectrum appeared to obtain more mates in female-biased groups (Table 2). A likelihood ratio test revealed a non-significant tendency for an overall interaction between sex ratio and exploration^2 (Chi-squared = 5.037, df = 2, p = 0.081). We explored this further by testing each sex ratio separately, and found that more extreme males mated with a higher number of females in female-biased groups (Est. ± SE = 0.452 ± 0.200; z-value = 2.261; p = 0.024), but not in even-sex ratio and male-biased groups (Table S4, Figure 1). Because male status was not a significant predictor of mating success in female-biased groups, and to reduce the number of covariates to avoid overfitting the model, we also ran a model for female-biased groups that did not include status and obtained similar results for exploration^2 (Est. ± SE = 0.542 ± 0.165; z-value = 3.276, p = 0.001). The model without status provided a better fit than the model with status (ΔAICc = 2.628). In addition, we tested whether the relationship between mating success and exploration score in female-biased groups could be predicted by status, running a GLMM with a gamma family and log link that included Normalized David's score (i.e. status) as the response, exploration, and exploration^2 as fixed effects, and individual identity as a random effect. We found that very fast-exploring and very slow-exploring males were more likely to be dominant in female-biased groups (Est. ± SE = 0.855 ± 0.356; z-value = 2.402, p = 0.016; Figure S6), indicating that the effect of exploration^2 detected in female-biased groups may be explained by male status. Unlike exploration, focal male boldness had no effect on number of mates (Table 2).

Table 2. Output of GLMMs examining the predictors of the number of mates obtained for males and females. The effects of exploration, exploration^2, boldness, status, and group sex ratio are reported for the models containing main effects only. Interactions between group sex ratio and focal phenotype are reported for the models containing both main effects and their interaction. (See text for details.)

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

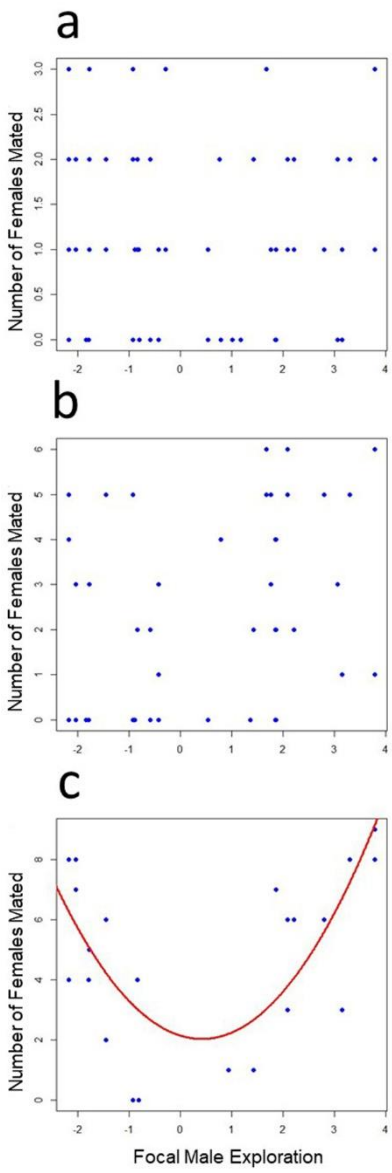

Figure 1. The relationship between the focal male's exploration and the number of females he mated with for **a)** male-biased, **b)** even sex ratio, and **c)** female-biased groups.

We then investigated the role of average competitor personality on the focal male's mating success by analyzing each sex ratio treatment separately. We found some evidence for social effects modulating precopulatory sexual selection on male exploration. In female-biased groups, there was an

interaction between the exploration of the focal male and the phenotypic composition of his competitive environment, in that faster-exploring males mated with more females when competitors were, on average, slower-exploring and *vice versa* (Figure 2a; Table 3). Although results were qualitatively similar when competitor exploration composition was defined as the proportion of fast-exploring competitors, this relationship was not significant (Table 3). Because models for female-biased groups were overfit (N = 24 with four fixed effects and one random effect), we re-ran models without male status. When male status was removed, the interaction between focal exploration and competitor exploration composition was significant both in the model where competitor phenotypic composition was defined as mean exploration and in the model where it was defined as the proportion of fast-explorers (Mean exploration: Est. ± SE = -0.351 ± 0.111; z-value = -3.167, p = 0.002; Proportion of Fast-explorers: Est. ± SE = -1.997 ± 0.750; z-value = -2.664, p = 0.008). Models without status provided better fits (lower AICcs) than models with status (Mean exploration: ΔAICc = 2.908; Proportion of Fast-explorers: ΔAICc = 2.508). We found no effect of competitors' phenotype in even sex ratio and male-biased groups (Table 3). 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, the proportion of fast-exploring males in the group, sex ratio, and the interaction between the two as fixed effects, and female group identity as a random effect. When tested against the intercept, we again 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 S5; Figure 2b). A likelihood ratio test comparing the full model with a model without the interaction between the proportion of fast-exploring males and sex ratio confirmed that the overall interaction was significant (Chi-squared = 26.84, df = 2, $p << 0.001$).

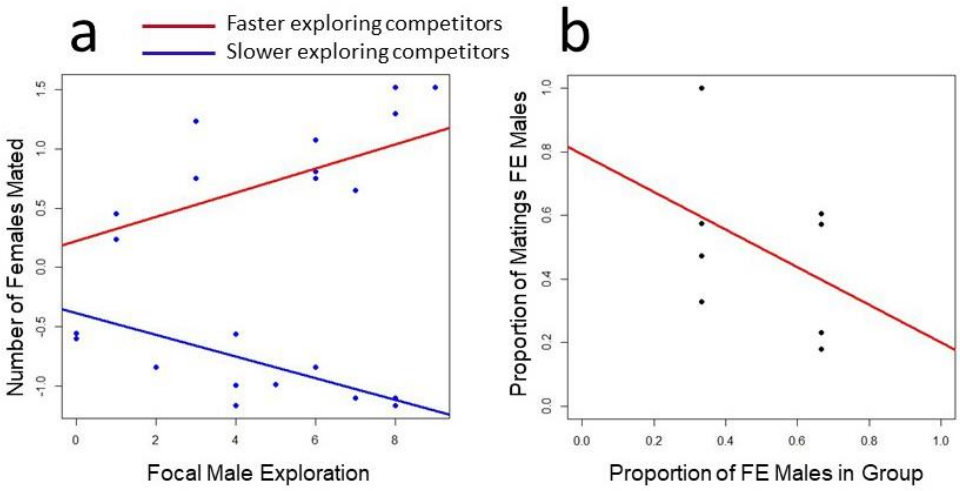

Figure 2. a) In female-biased groups, faster-exploring males obtained more mates when competitors were slower-exploring, on average, than the focal male, and slower-exploring males obtained more mates when competitors were faster-exploring, on average, than the focal male. **b)** In female-biased groups,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

Table 3. Output of GLMMs examining the effects of mean competitor personality and the proportion of fast-exploring competitors on the relationship between focal personality and number of mates obtained by males for three sex ratio treatments. (See text for details.)

Predictor	Est. ± SE	z-value	p
Mean competitor personality			
Male-Biased Groups (N=72)			
Focal Exploration	-0.045 ± 0.110	-0.405	0.685
Normalized David's Score	0.252 ± 0.106	2.363	**0.018**
Mean Competitor Exploration	-0.033 ± 0.111	-0.298	0.766
Focal * Mean Competitor Exploration	-0.066 ± 0.093	-0.712	0.476
Even Sex Ratio Groups (N=48)			
Focal Exploration	0.073 ± 0.107	0.688	0.492
Normalized David's Score	0.254 ± 0.110	2.302	**0.021**
Mean Competitor Exploration	-0.126 ± 0.112	-1.123	0.262
Focal * Mean Competitor Exploration	0.032 ± 0.097	0.332	0.740
Female-Biased Groups (N=24)			
Focal Exploration	-0.091 ± 0.195	-0.468	0.639
Normalized David's Score	0.096 ± 0.116	0.833	0.405
Mean Competitor Exploration	-0.063 ± 0.184	-0.342	0.733
Focal * Mean Competitor Exploration	-0.286 ± 0.136	-2.100	**0.036**
Proportion of fast-exploring competitors			
Male-Biased Groups (N=72)			
Focal Exploration (Binary)	-0.419 ± 0.684	-0.612	0.541
Normalized David's Score	0.256 ± 0.110	2.324	**0.020**
Proportion of Fast-Exploring Competitors	-0.902 ± 0.935	-0.964	0.335
Focal * Proportion of Fast-Exploring Competitors	0.563 ± 1.316	0.428	0.669
Even Sex Ratio Groups (N=48)			
Focal Exploration (Binary)	-0.642 ± 0.749	-0.857	0.391
Normalized David's Score	0.249 ± 0.112	2.220	**0.026**
Proportion of Fast-Exploring Competitors	-1.991 ± 1.190	-1.672	0.094
Focal * Proportion of Fast-Exploring Competitors	1.596 ± 1.405	1.136	0.256
Female-Biased Groups (N=24)			
Focal Exploration (Binary)	0.579 ± 0.555	1.043	0.297
Normalized David's Score	0.125 ± 0.115	1.085	0.278
Proportion of Fast-Exploring Competitors	0.476 ± 0.611	0.780	0.436
Focal * Proportion of Fast-Exploring Competitors	-1.423 ± 0.918	-1.549	0.121

Aim 2. Postcopulatory sexual selection

i) Polyandry. A female's exploration and boldness did not predict the number of males with whom she mated (i.e. her polyandry, Table 2). However, as expected, sex ratio predicted the overall levels of polyandry within groups, with the highest polyandry levels in male-biased groups and lowest average polyandry in female-biased groups (Table 2).

ii) Sperm competition intensity. In line with the effects of sex ratio on polyandry levels, sex ratio influenced the sperm competition intensity experienced by a male, being higher in male-biased groups and lower in female-biased groups, compared to even sex ratio groups (Table 4). Sperm

competition intensity was not predicted by boldness, but more dominant males experienced lower sperm competition intensity (Table 4). Furthermore, both faster- and slower-exploring males showed a tendency to experience lower sperm competition intensity than intermediate males in female-biased groups (Table 4). This quadratic relationship was not significant in the full model, and the interaction between exploration^2 and sex ratio was not significant as a whole (Chi-squared = 3.192, df = 2, p = 0.203). However, when we examined sex ratios separately, we found that males with more extreme exploration experienced lower sperm competition intensity in female-biased groups (Est. ± SE = -0.266 ± 0.114; z-value = -2.324; p = 0.020), but not even sex ratio or male-biased groups (Table S6; Figure 3). We also ran a model for female-biased groups that did not include status, given that status was not a significant predictor of sperm competition intensity in female-biased groups, and obtained similar results (Est. ± SE = -0.349 ± 0.106; z-value = -3.279, p = 0.001). However, the model with status provided a better fit (ΔAICc = 44.941). Furthermore, competitor exploration composition did not affect the relationship between a focal male's personality and his sperm competition intensity, regardless of whether competitor phenotypic composition was defined as mean competitor personality or proportion of fast competitors (Table 5).

Table 4. Output of GLMMs examining the predictors of male sperm competition intensity. The effects of exploration, exploration^2, boldness, status, and group sex ratio are reported for the models containing main effects only. Interactions between group sex ratio and focal phenotype are reported for the models containing both main effects and their interaction. (See text for details.)

Predictor	Est. ± 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 * Sex Ratio: Male-Biased	0.018 ± 0.051	0.351	0.726
Exploration * Sex Ratio: Female-Biased	-0.023 ± 0.068	-0.334	0.738
Exploration^2 * Sex Ratio: Male-Biased	-0.028 ± 0.057	-0.491	0.623
Exploration^2 * Sex Ratio: Female-Biased	-0.218 ± 0.121	-1.791	0.073
Boldness * Sex Ratio: Male-Biased	-0.005 ± 0.051	-0.107	0.915
Boldness * Sex Ratio: Female-Biased	-0.011 ± 0.076	-0.151	0.880
Status * Sex Ratio: Male-Biased	0.028 ± 0.053	0.531	0.595
Status * Sex Ratio: Female-Biased	0.073 ± 0.084	0.864	0.388

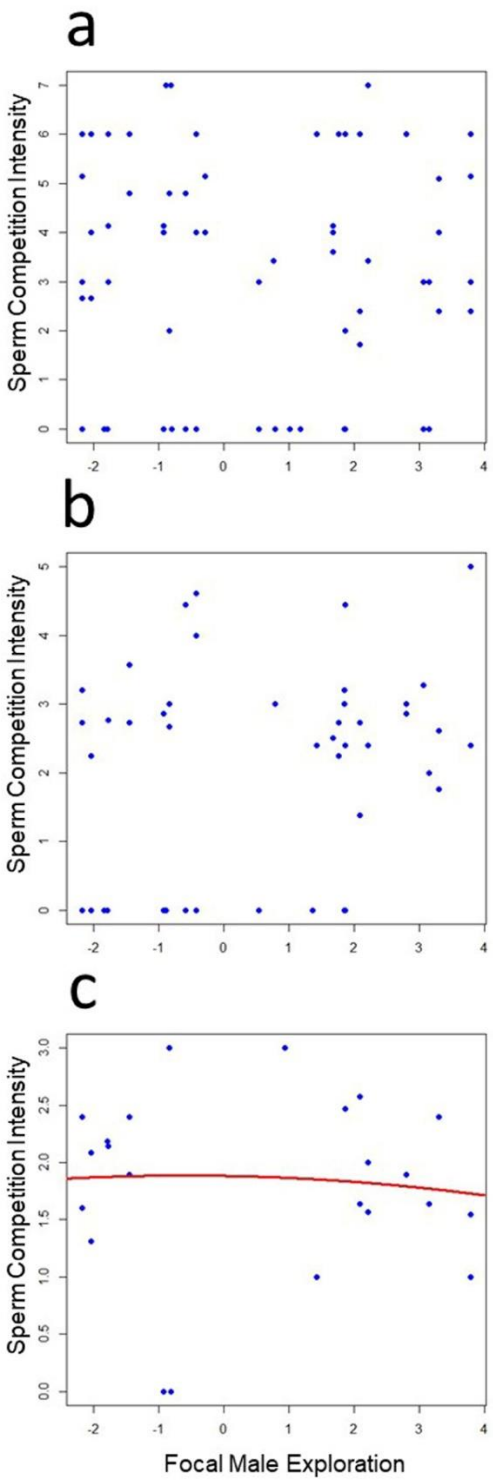

Figure 3. The relationship between the focal male's exploration and the sperm competition intensity he experiences for **a)** male-biased groups, **b)** even sex ratio groups, and **c)** female-biased groups.

Table 5. Output of GLMMs examining the effects of mean competitor personality and the proportion of fast-exploring competitors on the relationship between focal personality and the sperm competition intensity faced by males for three sex ratio treatments. (See text for details.)

Predictor	Est. ± SE	z-value	p
Mean competitor personality			
Male-Biased Groups (N=52)			
Focal Exploration	-0.002 ± 0.080	-0.031	0.976
Normalized David's Score	-0.042 ± 0.043	-0.959	0.337
Mean Competitor Exploration	0.036 ± 0.131	0.272	0.785
Focal * Mean Competitor Exploration	0.002 ± 0.032	0.058	0.953
Even Sex Ratio Groups (N=34)			
Focal Exploration	-0.100 ± 0.069	-1.444	0.149
Normalized David's Score	-0.118 ± 0.028	-4.179	**<0.001**
Mean Competitor Exploration	-0.127 ± 0.077	-1.656	0.098
Focal * Mean Competitor Exploration	-0.032 ± 0.022	-1.475	0.140
Female-Biased Groups (N=22)			
Focal Exploration	-0.256 ± 0.243	-1.057	0.291
Normalized David's Score	0.041 ± 0.027	1.537	0.124
Mean Competitor Exploration	-0.232 ± 0.249	-0.931	0.352
Focal * Mean Competitor Exploration	0.135 ± 0.080	1.679	0.093
Proportion of fast-exploring competitors			
Male-Biased Groups (N=52)			
Focal Exploration (Binary)	0.083 ± 0.285	0.292	0.771
Normalized David's Score	-0.041 ± 0.044	-0.937	0.349
Proportion of Fast-Exploring Competitors	-0.373 ± 0.718	-0.520	0.603
Focal * Proportion of Fast-Exploring Competitors	-0.327 ± 0.473	-0.691	0.490
Even Sex Ratio Groups (N=34)			
Focal Exploration (Binary)	-0.053 ± 0.213	-0.250	0.803
Normalized David's Score	-0.110 ± 0.028	-3.978	**<0.001**
Proportion of Fast-Exploring Competitors	-0.674 ± 0.473	-1.425	0.154
Focal * Proportion of Fast-Exploring Competitors	-0.298 ± 0.315	-0.946	0.344
Female-Biased Groups (N=22)			
Focal Exploration (Binary)	-0.526 ± 0.315	-1.669	0.095
Normalized David's Score	-0.004 ± 2.710e-05	-138.491	**<0.001**
Proportion of Fast-Exploring Competitors	-0.522 ± 0.462	-1.131	0.258
Focal * Proportion of Fast-Exploring Competitors	0.672 ± 0.447	1.504	0.133

iii) Remating rates. Across all sex ratios, dominant males had higher remating rates with individual females (Table 6). However, neither male personality nor group sex ratio predicted male remating rates (Table 6). Similarly, female personality, status, and group sex ratio did not predict female remating rates (Table 6).

Table 6. Output of GLMMs examining the predictors of remating rates for males and females. The effects of exploration, exploration^2, boldness, status, and group sex ratio are reported for the models containing main effects only. Interactions between group sex ratio and focal phenotype are reported for the models containing both main effects and their interaction. (See text for details.)

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

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_{rand} = 0.001; 95% range of simulated estimates = -0.139 - 0.072; Figure 4). While weak, results of randomization tests suggest that this effect was stronger than we would expect by chance, controlling for variance in male and female mating success. Furthermore, after performing a Bonferroni correction (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_{rand} = 0.302; 95% range of simulated estimates = -0.133 - 0.019).

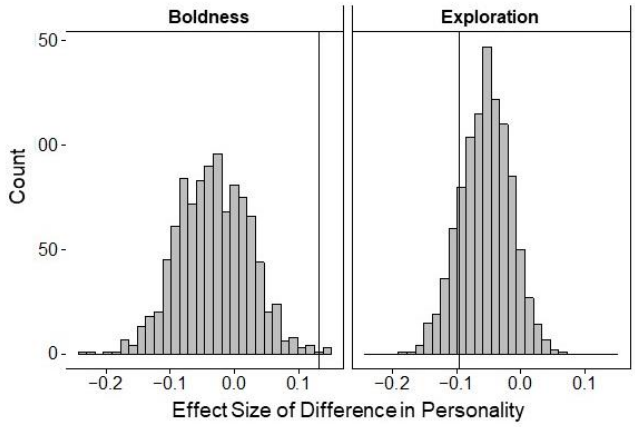

Figure 4. Individuals mate disassortatively with respect to boldness, but randomly with respect to exploration. Grey bars represent randomized distributions of effect sizes, and the vertical lines represent the empirical slopes.

Aim 4. Underpinning mechanisms

i) Solicitations. As expected, males received most solicitations in female-biased groups and fewest in male-biased groups (Table 7). Controlling for sex ratio treatment, we found that faster-exploring males and more dominant males received more solicitations than slower-exploring or subdominant males (Table 7; Figure 5a). There were no interactions between sex ratio and focal phenotype in predicting solicitations (Table 7). Furthermore, there was no evidence that mean competitor exploration influenced the relationship between male exploration and solicitations received in any sex ratio treatment (Table 8). Lastly, female personality and status had no effect on the number of solicitations given by a female (Table 7).

Table 7: Output of GLMMs examining the predictors of the number of solicitations received by males and the number of solicitations given by females. The effects of exploration, exploration^2, boldness, status, and group sex ratio are reported for the models containing main effects only. Interactions between group sex ratio and focal phenotype are reported for the models containing both main effects and their interaction. (See text for details.)

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

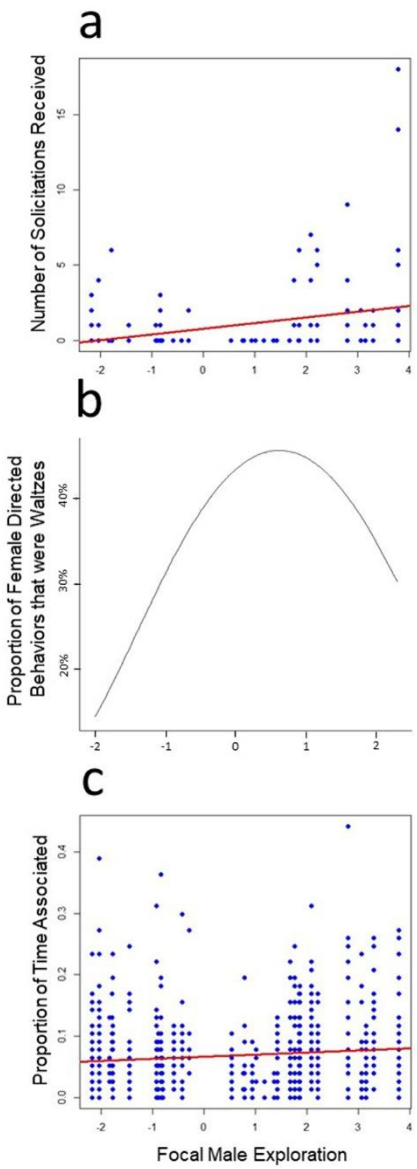

Figure 5. a) Faster-exploring males received more solicitations than slower-exploring males. **b)** Of the female-directed behaviors recorded (waltzing plus harassment), extreme exploring males had lower proportions of waltzes than intermediate exploring males. The plotted curve in this graph was based 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 spent slightly more time with females than slower-exploring males.

Table 8: Output of GLMMs examining the effects of mean competitor personality and the proportion of fast-exploring competitors on the relationship between a focal male's exploration and number of solicitations he received for three sex ratio treatments. (See text for details.)

Predictor	Est. ± SE	z-value	p
Mean competitor personality			
Male-Biased Groups (N=72)			
Focal Exploration	0.890 ± 0.389	2.310	0.021
Normalized David's Score	0.053 ± 0.334	0.160	0.873
Mean Competitor Exploration	0.224 ± 0.360	0.623	0.533
Focal * Mean Competitor Exploration	-0.443 ± 0.244	-1.818	0.069
Even Sex Ratio Groups (N=48)			
Focal Exploration	1.700 ± 0.565	3.009	0.002
Normalized David's Score	0.646 ± 0.248	2.606	**0.009**
Mean Competitor Exploration	-0.859 ± 0.642	-1.338	0.181
Focal * Mean Competitor Exploration	1.120 ± 0.602	1.860	0.063
Female-Biased Groups (N=24)			
Focal Exploration	0.312 ± 0.380	0.821	0.412
Normalized David's Score	0.624 ± 0.222	2.805	**0.005**
Mean Competitor Exploration	-0.152 ± 0.356	-0.426	0.670
Focal * Mean Competitor Exploration	-0.178 ± 0.250	-0.710	0.477
Proportion of fast-exploring competitors			
Male-Biased Groups (N=72)			
Focal Exploration (Binary)	1.366 ± 2.506	0.545	0.586
Normalized David's Score	0.175 ± 0.565	0.309	0.757
Proportion of Fast-Exploring Competitors	-0.172 ± 3.992	-0.043	0.966
Focal * Proportion of Fast-Exploring Competitors	-0.633 ± 4.457	-0.142	0.887
Even Sex Ratio Groups (N=48)			
Focal Exploration (Binary)	-0.045 ± 2.334	-0.019	0.985
Normalized David's Score	0.754 ± 0.568	1.326	0.185
Proportion of Fast-Exploring Competitors	-1.468 ± 4.001	-0.367	0.714
Focal * Proportion of Fast-Exploring Competitors	3.364 ± 4.201	0.801	0.423
Female-Biased Groups (N=24)			
Focal Exploration (Binary)	2.250 ± 1.055	2.134	0.033
Normalized David's Score	0.512 ± 0.212	2.413	**0.016**
Proportion of Fast-Exploring Competitors	1.361 ± 1.144	1.190	0.234
Focal * Proportion of Fast-Exploring Competitors	-2.122 ± 1.633	-1.299	0.194

ii) Proportion of female-directed behaviors that were waltzes. We found that, regardless of sex ratio treatment, of the total number of female-directed behaviors (i.e. waltzes plus harassments), males with more extreme exploration scores expressed lower proportions of waltzes, compared to males with intermediate exploration (Table 9; Figure 5b). Subdominant males also showed lower proportions of waltzes over the total number of female-directed behaviors, compared to more dominant males (Table 9). Furthermore, our results suggested that subdominant males displayed lower proportions of waltzes over the total number of female-directed behaviors in female-biased groups, compared to even sex ratio groups and bolder males expressed lower proportions of waltzes over the

total number of female-directed behaviors in male-biased groups, compared to even sex ratio groups (Table 9). While the interaction between male boldness and sex ratio (Chi-squared = 8.420, df = 2, p = 0.015) was significant as a whole, the interaction between status and sex ratio was weaker (Chi-squared = 5.903, df = 2, p = 0.052). When we examined each sex ratio in isolation, we found that in male- and female-biased groups, but not even sex ratio groups, more dominant males gave higher proportions of waltzes over the total number of female-directed behaviors (Table S7). Despite the significant overall effect of the interaction between boldness and sex ratio, we found that boldness did not predict the proportion of female-directed behaviors that were waltzes in any of the sex ratios (Table S7). Furthermore, although exploration^2 was a significant predictor of the proportion of waltzes over the total number of female-directed behaviors in the inclusive model, there was no interaction between exploration^2 and sex ratio in the inclusive model, and exploration^2 was not a significant predictor of the proportion of waltzes when we tested individual sex ratios separately (Tables 9 & S7). We also ran a model for female-biased groups that did not include exploration or exploration^2 and obtained similar results for boldness and status (Boldness: Est. ± SE = 0.001 ± 0.227; z-value = 0.004, p = 0.997; Status: Est. ± SE = 0.561 ± 0.128; z-value = 4.380; p < 0.001). This simpler model provided a better fit than the model with exploration and exploration2 (ΔAICc = 8.659).

iii) Associations. We found that: 1) males spent more time with the females with whom they remated more frequently, 2) faster-exploring and dominant males associated more with females, regardless of how often they mated with these females, than did slower-exploring or subdominant males (Figure 5c), and 3) the highest number of associations was between faster-exploring males and the females with whom they mated (Table 9). Lastly, males spent more time associating with females in female-biased groups, compared to even sex ratio treatments (Table 9).

Table 9: Output of GLMMs examining the predictors of the proportion of waltzes over the total number of female-directed behaviors (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). Main effects are reported for the models containing only these predictors. Interaction effects are reported for the models containing both main effects and their interaction. (See text for details.)

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

Discussion

While sexual selection has been suggested as a fundamental process modulating variation of personality in populations, little is known about the extent to, and the way in which sexual selection targets personality traits. Using 24 replicate groups of red junglefowl, we experimentally manipulated sex ratio and exploration composition and examined the roles of personality on pre- and postcopulatory sexual selection, polyandry, assortative mating, and the behavioral mechanisms that may govern these patterns. In addition to examining the effects of focal individuals' personality on mating performance, we also explored group-level effects by analyzing the influence of competitor personality composition.

We found that a tendency to explore a novel environment did not correlate with a tendency to investigate a novel object, in male or female red junglefowl, in our study population. Similar results have been found in fowl (Favati et al., 2016; 2018), as well as in mountain chickadees (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 (David et al., 2011). Furthermore, ecological conditions may affect whether correlations between behavioral traits are selected for (Bell & Sih, 2007; Dingemanse et al., 2007). For example, different populations of three-spined sticklebacks, *Gasterosteus aculeatus*, have been shown to vary in correlations between activity, aggressiveness, and exploratory behavior due to differences in the size and predation pressure of home ponds (Dingemanse et al., 2007). Although among-individual correlations between different behavioral traits may influence the net selective forces operating on each trait (Lande & Arnold, 1983; Dochtermann & Dingemanse, 2013), the lack of correlation between behavioral traits in our study suggests that sexual selection operating on exploration in our population of red junglefowl acts independently of any potential selection operating on boldness.

We also found some evidence to suggest weak linear relationships between personality and status in both sexes. We found a weak negative correlation between female exploration and status, suggesting slower-exploring females were more dominant. We also found some evidence to suggest that shyer individuals of both sexes were more dominant, although for females, correlations between boldness and status were only observed in male-biased groups. In domestic fowl, previous work has demonstrated that faster-exploring males are more likely to be dominant, however, this relationship was only seen in dyadic contests; in larger groups, neither boldness nor exploration was found to predict social rank (Favati et al., 2014a; 2017). In other species, the relationship between personality and social status is inconsistent, with faster explorers dominating slower explorers in some studies (Verbeek et al., 1996; Cole & Quinn, 2011; David et al., 2011), and *vice versa* in others (Fox et al., 2009). Similarly, bolder individuals sometimes dominate shyer individuals in some studies

(Sundström et al., 2004; Colléter & Brown, 2011; Dahlbom et al., 2011), and *vice versa* in others (Taylor & Lattanzio, 2016). Moreover, relationships between personality and status may be context-dependent (Dingemanse & de Goede, 2004). For example, in great tits, faster-exploring, territorial males may be dominant over slower-exploring territorial males, while slower-exploring, non-territorial juvenile males may have higher status than their faster-exploring counterparts (Dingemanse & de Goede, 2004). Although behavioral differences may arise as a result of dominance relationships (Arakawa, 2006; Barnard & Luo, 2002; Favati et al 2014b), personality may also drive patterns of social status (Schjolden et al., 2005; Fox et al., 2009). 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 behavioral traits examined in our study correlate with a trait we did not examine, like aggression, which has a strong influence on social status in fowl (Favati et al., 2014a; 2017; Pizzari & McDonald, 2019) as well as in other species (e.g. Verbeek et al., 1996; Pottinger & Carrick, 2001; Armitage & van Vuren, 2003; Bolhuis et al., 2005). Favati et al. (2017) demonstrate that boldness, but not exploration, correlates positively with aggression in male domestic fowl. Lastly, correlations between personality and social status may exist if personality influences response 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, when in a group setting (Verbeek et al., 1996; Verbeek et al., 1999). In male domestic fowl, however, winner-loser effects may not predict social rank (Favati et al., 2017). Thus, any influence personality may have on social defeat is unlikely to influence status in male domestic fowl, and potentially red junglefowl as well. The evidence of possible relationships between male personality and status in red junglefowl detected in our study is especially important given that, consistent with previous studies on

red junglefowl (Lill, 1966; Thornhill, 1988; Collias & Collias, 1996; Kim & Zuk, 2000; Pizzari & McDonald, 2019), we found that status often predicted male mating performance.

We found little evidence for male boldness, *per se*, playing an important role in sexual selection although it should be noted that male boldness was only weakly repeatable, and not significantly so. 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 than intermediate males. Our results are consistent with past work in red junglefowl showing that males, which obtain more mates also suffer lower sperm competition intensity (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). Furthermore, bolder males had increased reproductive success later in life, compared to shyer males. Similarly, active-aggressive males were shown to have higher mating success than less active-aggressive or hyperaggressive males in water striders (Sih et al., 2014). Sih et al. (2014) propose that this may result from more active aggressive males spending more time searching for mates. Overall, our results indicate that, in female-biased groups, males at both exploration extremes have higher mating performance and face lower sperm competition, suggesting that, in female-biased groups, disruptive pre- and postcopulatory sexual selection may result in extremely fast- and slow-exploring males contributing more to future generations than males of intermediate phenotype.

Mating advantages for extreme males may arise as a result of inherent differences between extreme and intermediate-exploring males in mating strategy or social status. For example, we found that, of the total number of female-directed behaviors (waltzing and harassment), males at both extremes of the exploration spectrum expressed lower proportions of waltzes than intermediate-exploring males. Waltzing is likely related to courtship, whereas harassment reflects sexual coercion

(Zuk et al., 1990; Johnsen et al., 1995), suggesting that, in our population, extreme exploring males might pursue different reproductive strategies from intermediate-exploring males. Furthermore, we found that in female-biased groups, very fast- and very slow-exploring males were more likely to achieve high social status than intermediate-exploring males. It is possible that, in female-biased groups, males with extreme exploration scores attained more mates by achieving higher status, given that social status often predicts male mating performance in red junglefowl (Lill, 1966; Thornhill, 1988; Collias & Collias, 1996; Kim & Zuk, 2000; Pizzari & McDonald, 2019). The fact that male status did not predict mating success in female-biased groups may, therefore, be due to male exploration masking the effects of status. On the other hand, competition among males may be reduced in female-biased groups, relaxing selection on status and allowing personality to become relevant, as mating patterns are largely female-driven under such sex ratios (Løvlie & Pizzari, 2007). These results however, must be taken with caution; we were limited in sample size, which often resulted in overfit models when we examined female-biased sex ratios in isolation. We tried to limit this issue by reducing the number of fixed and random effects present in our models, however, we suggest future studies focus on investigating female-biased groups in more depth.

In addition to intrinsic differences between extreme and intermediately exploring males, dissimilar male exploration types may acquire mating advantages via disparate channels. For example, slower-explorers may gain an advantage by staying in areas with higher female density (e.g. feeding sites), leading to increased opportunities for mating. In contrast, faster-explorers may cover a greater spatial area to encounter more females. Faster-explorers may also be more willing to follow females as they move, leading to increased mating performance. This is supported by the fact that, in addition to finding that faster-exploring males associated most with the females with whom they mated more frequently, faster-exploring males were also generally more likely to associate with females, compared to slower-exploring males. Because past work on this population has suggested that pairs that spend more time associating are more likely to mate (McDonald & Pizzari pers. comm.), faster-exploring males may gain a mating advantage by spending more time associating with females, compared to

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

Interestingly, in our study, a male's mating performance also appeared to be affected by the exploration composition of his competitors. In female-biased groups, but not in groups with an even sex ratio or in male-biased groups, faster-exploring males attained more mates when competitors were slower-exploring on average and *vice versa*. In water striders, group personality composition has been shown to affect the number of mates, total number of copulations, proportion of time spent mating, and average duration of copulations in males (Sih et al., 2014). In this system, individual mating performance was reduced when a hyper-aggressive male was present in the group. In contrast to our results, however, in water striders, the effects of group personality composition on mating performance was not found to depend on the focal individual's phenotype (Sih et al., 2014). We also found that in female-biased groups, faster-exploring males obtained a higher proportion of matings 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 selection. Negative frequency dependent sexual selection may contribute to the maintenance of interindividual variation in exploration, in that, when the number of faster-explorers increases, slower-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 over common type males, potentially given female habituation to cues given by common type males (reviewed in Knoppien, 1985). It is important to note, however, that when trait distributions are continuous, rather than bimodal, as was the case for the behavioral traits examined in our study, a challenge to testing for negative frequency dependence is that phenotypes are categorized by binning variables based on

arbitrary cutoffs. In this study we chose to bin individuals with personality scores greater than zero as fast or bold and less than zero as slow or shy. Nevertheless, analyses based on mean group personality were, qualitatively, largely consistent with models using proportions of personality categories. The results of our study present some of the first lines of evidence to suggest that individual mating performance may be related to the frequency of personality types in a group. Moreover, the fact that social conditions favored rare extreme phenotypes with respect to male exploration in our study may help explain the quadratic relationship seen between focal exploration and male mating success.

In addition to finding that faster-exploring males received a higher number of solicitations from females, females also showed a preference for dominant males, which supports past work (Lill, 1966; Thornhill, 1988; Pizzari & Birkhead, 2000). Moreover, there was also some evidence to suggest that male boldness affected male mating strategy in our study. Of the total number of female-directed behaviors observed (waltzing and harassment) in male-biased groups, shyer males displayed higher proportions of waltzes, compared to bolder males. From the pre- and postcopulatory measures of success recorded in this study, however, it did not appear that shyer males gained a mating advantage by employing this strategy. Several previous studies have demonstrated links between male personality and male mating strategy (Reaney & Backwell, 2007; Patrick et al., 2011) and/or female preference (Godin & Dugatkin, 1996; Reaney & Backwell, 2007; Schuett et al., 2011; Dzieweczynski et al., 2013; Teyssier et al., 2014). For example, in one population of the socially monogamous great tit, faster-exploring males were found to put more effort into extrapair paternity while slower-exploring males invested more in within pair paternity (Patrick et al., 2011; but see Araya-Ajoy et al. 2016; Abbey-Lee et al. 2018; Roth et al., in press). Nevertheless, in this population, variation in total paternity (i.e. within pair plus extrapair paternity) was found to be unaffected by personality, suggesting that these routes of paternity are alternative strategies employed by males with different personality types (Patrick et al., 2011). Similarly, bolder male fiddler crabs have been shown to court females more than shyer males (Reaney & Backwell, 2007). In this species, bolder males appear to gain a mating advantage, obtaining more mates and winning female preference (Reaney & Backwell,

2007). Male personality has been also shown to predict female choice in several other species (Godin & Dugatkin, 1996; Schuett et al., 2011; Dzieweczynski et al., 2013; Teyssier et al., 2014). For example, females appear to 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).

Although we found no assortative or disassortative mating with respect to exploration, we found that individuals tended to mate disassortatively with respect to boldness. Our findings are consistent with work in other species showing a tendency to mate with dissimilar personality types. In great tits, individuals older than one year of age have been shown to mate disassortatively with respect to exploration behavior (Dingemanse et al., 2004). Interestingly though, Both et al. (2005) found that assortative pairs of great tits produced higher quality fledglings than disassortative pairs. It may be the case that tits of intermediate exploration have higher lifetime fitness due to temporal fluctuations in selective pressures (Dingemanse et al., 2004; Both et al., 2005). In contrast to our findings, bridge spiders, *Larinioides sclopetarius*, and Eastern bluebirds, *Sialia sialis*, mate assortatively with respect to aggression (Kralj-Fišer et al., 2013; Harris & Siefferman, 2014). 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.

Overall, we present evidence suggesting that both pre- and post-copulatory sexual selection may target male personality in a captive population of red junglefowl, particularly in female-biased groups where males with extremely high and low exploration have an advantage. We also show that the personality composition of a group modulates the way sexual selection affects the personality of focal males (e.g. fast exploring males are particularly favored when their competitors are, on average, slower exploring) suggesting negative frequency dependent selection. 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 underpinning these personality traits in this species. However, because we did not assess paternity in the current study, it is important to note that we are limited in the conclusions we can draw regarding the effects of male personality on reproductive success. We suggest that future work be conducted to shed light on such potential relationships.

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Supplementary Information

APPENDIX 1

```
# function to get boostraping "percentile" CI - only one random effect is allowed
# we use the case boostrap (fully non-parametric)


#' Title
#'
#' @param model: put a lmer model
#' @param bootN: the number of boostrapping (defaul = 1000), but you could increase to 10,000 for your real results
#'
#' @return
#' @export
#'
#' @examples
nonpara_boot <- function(model, bootN = 1000){

  # helper function for boostrap()
  my_get <- function(model) {
    beta <- getME(model, "beta")
    sigma <- getME(model, "sigma")
    sigma2 <- sigma^2
    tau2 <- unname(sigma * getME(model, "theta"))^2
    rep <- tau2/(tau2 + sigma2)
    c(beta = beta, sigma2 = sigma2,  tau2 = tau2, rep = rep)
  }

  # boostrapping - type = "case" fully
  # we are only respmpleing "individual" - resample = c(TRUE, FALSE)
  #  for why - see "Van der Leeden, R., Meijer, E. and Busing F. M. (2008) Resampling multilevel models. In J. de Leeuw
and E. Meijer, editors, Handbook of Multilevel Analysis, pages 401–433. New York: Springer."
  # The book chapter says "The cases bootstrap, finally, requires minimal assumptions: Only the hierarchical dependency in
the data is assumed to be specified correctly."
  boot_res <- lmeresampler::bootstrap(model = model, fn = my_get, type = "case", B = bootN, resample = c(TRUE, FALSE))
  # get the CI for everything
  paraN <- length(boot_res$t0)

  # percetile CI does not assume normality and has other good properties
  ind_fun <- function(index){boot.ci(boot_res, index = index, type = c("norm", "basic", "perc"))}
  # get the list of CI results
  ci_list <- map(1:paraN, ind_fun)
  # get values
  ci_value <- map(ci_list, "normal")

  # getting lower and upper limits
  ci_low <- flatten_dbl(map(ci_value, 2))
  ci_upr <- flatten_dbl(map(ci_value, 3))

  # getting names of the parameters
  Name <- c(names(fixef(model)), names(boot_res$t0)[-(1:length(names(fixef(model))))])

  # putting all togther
  res <- tibble(Name = Name, Est = as.numeric(boot_res$t0) , CI_L = ci_low, CI_U =  ci_upr)
  return(res)

}
```

APPENDIX 2

To obtain a single exploration score and a single boldness score for each individual, we ran GLMs to control for fixed effects, following the methods presented in Quinn et al. (2009). For exploration, we ran a model for each sex with PC1 as our response variable and individual identity, age, trial number, days since March 1st, and whether it was a morning or evening trial as fixed effects. We included trial number to control for potential habituation across replicates (Dingemanse et al., 2002; Quinn et al., 2009). We included the number of days past March 1st in which the trial occurred, as exploration has been shown to change over the season in some species (Dingemanse et al., 2002; Quinn et al., 2009). We included time of day (morning vs. evening) since exploration may change over the course of the day. We did not include year, as the only individuals that were tested for the first time in 2017 were first year females, so it would have been impossible to distinguish between the potential effects of age and year. We used AICc to select the best model and determine which fixed effects to retain. For females, the model that included individual identity, number of days past March 1st in which the trial occurred, and whether it was a morning or evening trial as fixed effects had the lowest AICc (Table S8). We therefore used this model to calculate an exploration score for each female. For males, the model that included individual identity and whether it was a morning or evening trial as fixed effects had the lowest AICc (Table S9). Given this, we used this model to calculate an exploration score for each male. We obtained a single exploration score for each individual by adding the intercept coefficient to the parameter for a given individual. To obtain a single boldness score for each individual, we included individual identity, age, trial number, the number of days past March 1st in which the trial began, and whether the novel object or baseline trial came first as fixed effects. We used AICc to determine which fixed effects to retain. For both sexes, the model that contained individual identity alone produced the best fit (Tables S10 & S11). We added the intercept coefficient to the parameter for a given individual to formulate a single boldness score for each individual.

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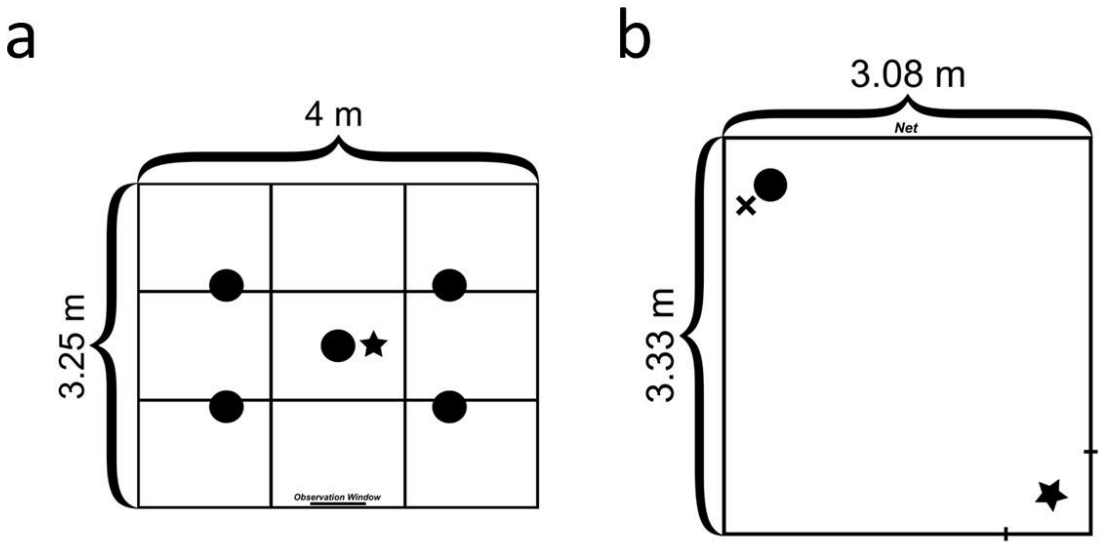

Figure S1. a) Layout of the novel arena room. The five circles represent artificial trees. The star represents the starting point of individuals. Beige masking tape was used to create the quadrats. **b)** Layout of the novel object pen. The circle represents the reward bowl, placed 50 cm from the upper left-hand corner. During trials in which the novel object was present, the rubber duck was placed 2 cm to the left of the bowl where the "x" is. The two ticks in the lower right-hand corner represent the markings (88 cm from the corner) in which the cardboard carrier box (see star) was lined up to release individuals. The pen had a net on one side and opaque Tarpaulin on the remaining three sides.

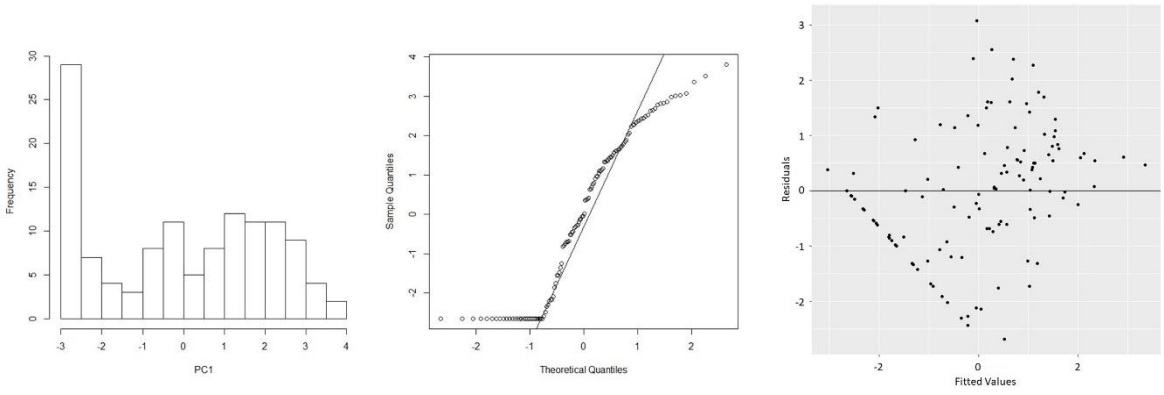

Figure S2. For females, PC1 of the novel arena assay measures had nonnormal, continuous distributions. Higher PC1 values indicate more exploratory individuals.

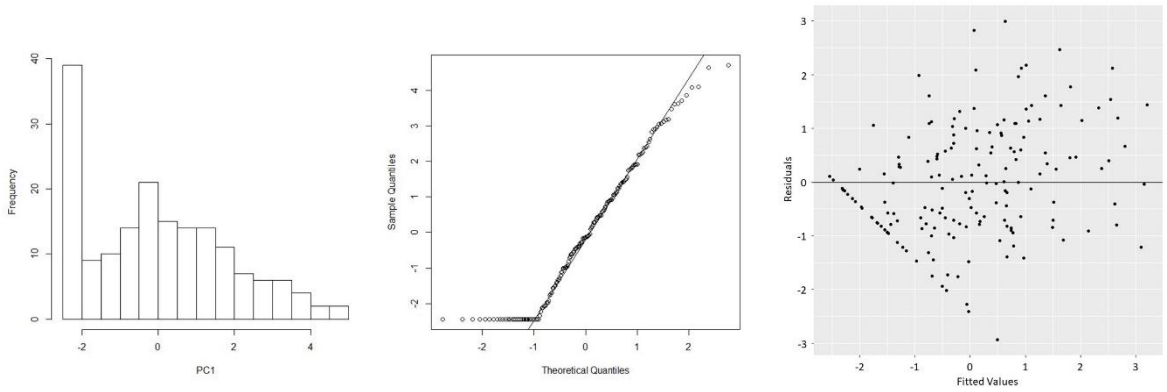

Figure S3. For males, PC1 of the novel arena assay measures had nonnormal, continuous distributions. Higher PC1 values indicate more exploratory individuals.

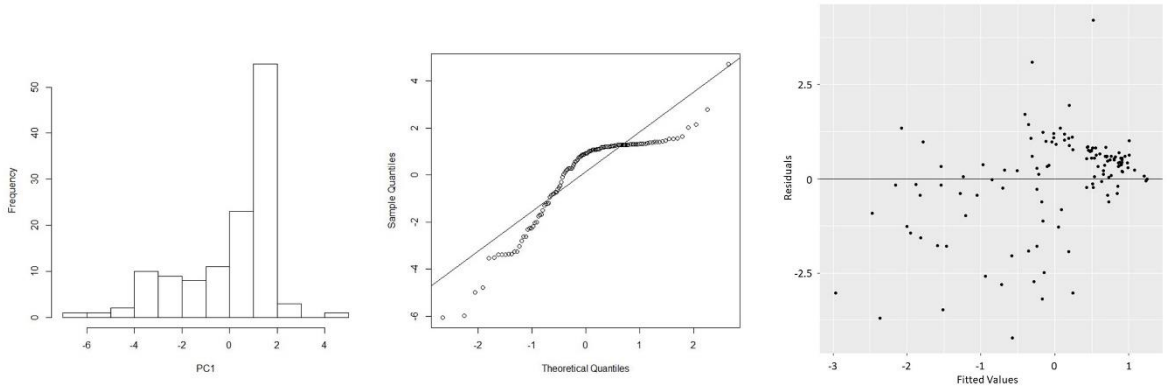

Figure S4. For females, PC1 of the novel object assay measures had nonnormal, continuous distributions. Higher PC1 values indicate bolder individuals (i.e. those who were faster to move towards the novel object).

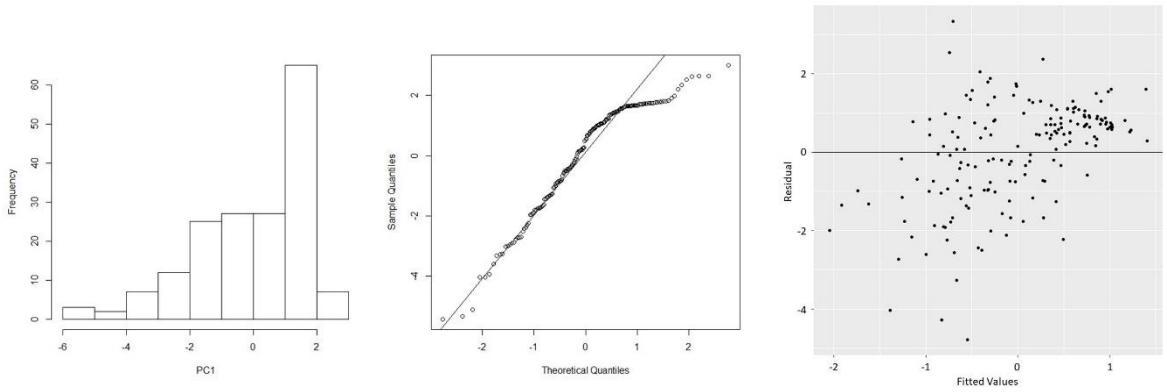

Figure S5. For males, PC1 of the novel object assay measures had nonnormal, continuous distributions. Higher PC1 values indicate bolder individuals (i.e. those who were faster to move towards the novel object).

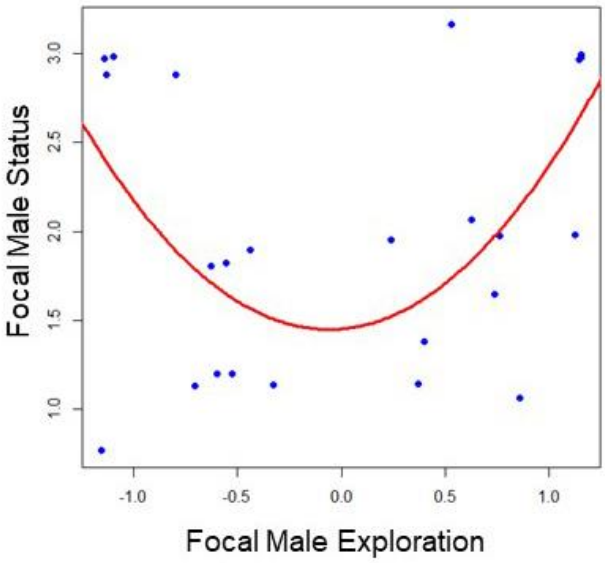

Figure S6. Very fast- and very slow-exploring males were more likely to be dominant in female-biased groups.

Table S1. Outputs of generalized linear mixed models examining the predictors of status in males and females. The outputs for exploration, boldness, and group sex ratio are reported for the models containing main effects only. The outputs for all two-way interactions between main effects are reported for the models containing both main effects and the interaction between them. (See text for details.)

Predictor	Est. ± SE	z-value	p
Males (N=144)			
Exploration	0.074 ± 0.089	0.833	0.405
Boldness	-0.159 ± 0.072	-2.210	**0.027**
Sex Ratio: Male Biased	0.459 ± 0.087	5.270	<**0.001**
Sex Ratio: Female Biased	-1.076 ± 0.124	-8. 675	<**0.001**
Exploration * Sex Ratio: Male Biased	0.014 ± 0.097	0.146	0.884
Exploration * Sex Ratio: Female Biased	0.099 ± 0.140	0.711	0.477
Boldness * Sex Ratio: Male Biased	-0.085 ± 0.095	-0.896	0.370
Boldness * Sex Ratio: Female Biased	-0.235 ± 0.144	-1.626	0. 104
Exploration * Boldness	0.056 ± 0.086	0.654	0.513
Females (N=138)			
Exploration	-0.324 ± 0.118	-2.745	**0.006**
Boldness	-0.102 ± 0.085	-1.193	0.233
Sex Ratio: Male Biased	-1.043 ± 0.132	-7.884	<**0.001**
Sex Ratio: Female Biased	0.484 ± 0.093	5.176	<**0.001**
Exploration * Sex Ratio: Male Biased	-0.051 ± 0.159	-0.324	0.746
Exploration * Sex Ratio: Female Biased	0.090 ± 0.084	1.078	0.281
Boldness * Sex Ratio: Male Biased	-0.500 ± 0.164	-3.053	**0.002**
Boldness * Sex Ratio: Female Biased	-0.001 ± 0.091	-0.015	0.988
Exploration * Boldness	-0.167 ± 0.105	-1.590	0.112

Table S2. Outputs of generalized linear mixed models examining whether a sex difference exists in behavioral measures recorded in novel arena and novel object assays. The models are tested against a female intercept. (See text for details.)

Predictor	Est. ± SE	z-value	p
Novel Arena (N=298)			
Latency to unfreeze	0.089 ± 0.135	0.660	0.512
Latency to leave starting quadrat	-0.092 ± 0.135	-0.680	0.495
Latency to visit six quadrats	-0.348 ± 0.195	-1.790	0.073
Number of quadrats visited	-0.142 ± 0.124	-1.145	0.252
Number of transitions between quadrats	-0.781 ± 0.666	-1.173	0.241
Novel Object (N=299)			
Latency to 0.5 m in the novel object trial	-0.185 ± 0.335	-0.552	0.581
Latency to one body length in the novel object trial	-0.505 ± 0.319	-1.584	0.113
Latency to feed in the novel object trial	-0.058 ± 0.275	-0.213	0.832
Difference novel object and baseline in latency to 0.5 m	0.155 ± 0.045	3.460	**0.001**
Difference novel object and baseline in latency to one body length	-0.033 ± 0.061	-0.540	0.587
Difference novel object and baseline in latency to feed	-0.104 ± 0.061	-1.720	0.086

Table S3. Patterns of the number of successful copulations and the number of solicitations observed for all groups and for groups within each sex ratio. (See text for details.)

	Total Number	Range Across Groups	Mean ± SD Across Groups
Number of successful copulations			
All groups	929	8-67	38.708 ± 16.112
Male-biased groups	244	8-56	30.500 ± 18.111
Even sex ratio groups	321	26-57	40.125 ± 10.218
Female-biased groups	364	21-67	45.500 ± 16.987
Number of solicitations			
All groups	136	0-18	5.667 ± 4.896
Male-biased groups	19	0-6	2.375 ± 2.134
Even sex ratio groups	27	1-6	3.375 ± 1.847
Female-biased groups	90	6-18	11.25 ± 4.097

Table S4. Outputs of generalized linear mixed models examining the effects of exploration, exploration^2, and status on the number of females a male mated with for each sex ratio treatment. (See text for details.)

Predictor	Est. ± SE	z-value	p
Male Biased Groups (N=72)			
Focal Exploration	-0.012 ± 0.095	-0.130	0.896
Focal Exploration^2	0.111 ± 0.090	1.232	0.218
Status	0.213 ± 0.105	2.024	**0.043**
Even Sex Ratio Groups (N=48)			
Focal Exploration	0.122 ± 0.107	1.132	0.258
Focal Exploration^2	0.030 ± 0.110	0.272	0.786
Status	0.241 ± 0.105	2.286	**0.022**
Female Biased Groups (N=24)			
Focal Exploration	0.026 ± 0.093	0.281	0.779
Focal Exploration^2	0.452 ± 0.200	2.261	**0.024**
Status	0.100 ± 0.125	0.803	0.422

Table S5. Outputs of generalized linear mixed models examining the effects the proportion of fast-exploring males in a group, sex ratio, and their interaction on the proportion of matings obtained by fast-exploring males in each group (N=24). (See text for details.)

Predictor	Est. ± SE	z-value	p
Proportion of fast-exploring males	9.152 ± 1.937	4.724	**<0.001**
Sex Ratio: Male-Biased	1.590 ± 1.697	0.937	0.349
Sex Ratio: Female-Biased	4.364 ± 1.242	3.514	**<0.001**
Proportion of fast-exploring males * Sex Ratio: Male-Biased	-4.907 ± 3.188	-1.539	0.123
Proportion of fast-exploring males * Sex Ratio: Female-Biased	-10.781 ± 2.170	-4.968	**<0.001**

Table S6. Outputs of generalized linear mixed models examining the effects of exploration, exploration^2, and status on the sperm competition intensity experienced by a male for each sex ratio treatment. (See text for details.)

Predictor	Est. ± SE	z-value	p
Male Biased Groups (N=72)			
Focal Exploration	-0.014 ± 0.047	-0.302	0.763
Focal Exploration^2	-0.014 ± 0.039	-0.349	0.727
Status	-0.041 ± 0.043	-0.937	0.349
Even Sex Ratio Groups (N=48)			
Focal Exploration	-0.008 ± 0.043	-0.180	0.857
Focal Exploration^2	0.051 ± 0.035	1.456	0.145
Status	-0.120 ± 0.030	-3.989	**<0.001**
Female Biased Groups (N=24)			
Focal Exploration	-0.042 ± 0.099	-0.427	0.670
Focal Exploration^2	-0.266 ± 0.114	-2.324	**0.020**
Status	0.021± 0.013	1.583	0.113

Table S7. Outputs of generalized linear mixed models examining the effects of exploration, exploration^2, boldness, and status on the proportion of waltzes over the total number of female-directed behaviors (waltzes plus harassments) displayed by a male for each sex ratio treatment. (See text for details.)

Predictor	Est. ± SE	z-value	p
Male Biased Groups (N=72)			
Focal Exploration	0.014 ± 0.125	0.109	0.913
Focal Exploration^2	-0.104 ± 0.062	-1.692	0.091
Boldness	-0.155 ± 0.127	-1.223	0.221
Status	0.257 ± 0.088	2.915	**0.004**
Even Sex Ratio Groups (N=48)			
Focal Exploration	-0.059 ± 0.151	-0.391	0.696
Focal Exploration^2	-0.111 ± 0.084	-1.319	0.187
Boldness	-0.088 ± 0.138	-0.634	0.526
Status	0.058 ± 0.072	0.806	0.420
Female Biased Groups (N=24)			
Focal Exploration	-0.014 ± 0.225	-0.060	0.952
Focal Exploration^2	0.055 ± 0.357	0.155	0.877
Boldness	-0.013 ± 0.252	-0.051	0.959
Status	0.549 ± 0.157	3.507	**<0.001**

Table S8. We explored how PC1 of a novel arena assay conducted on females was affected by individual identity, age, trial number (Trial), days since March 1st (Date), and whether the trial occurred in the morning or evening (Morning/Evening). We always retained individual identity in our models. For the other fixed effects, we conducted model selection, via second-order Akaike Information Criterions (AICc). The model that included individual identity, number of days past March 1st in which the trial occurred, and whether it was a morning or evening trial as fixed effects had the lowest AICc. (See supplementary text for details.)

Additional Terms in Model	AICc	ΔAICc
Trial, Date, Age, Morning/Evening	513.284	5.753
Date, Age, Morning/Evening	510.707	3.176
Trial, Age, Morning/Evening	521.095	13.564
Trial, Date, Morning/Evening	512.123	4.592
Trial, Date, Age	524.225	16.694
Date, Age	522.097	14.566
Date, Morning/Evening	**507.531**	**0**
Age, Morning/Evening	520.190	12.659
Trial, Age	529.260	21.729
Trial, Morning/Evening	516.901	9.37
Trial, Date	523.893	16.362
Date	519.417	11.886
Trial	524.780	17.249
Age	526.462	18.931
Morning/Evening	516.033	8.502
No additional terms	522.764	15.233

Table S9. We explored how PC1 of a novel arena assay conducted on males was affected by individual identity, age, trial number (Trial), days since March 1st (Date), and whether the trial occurred in the morning or evening (Morning/Evening). We always retained individual identity in our models. For the other fixed effects, we conducted model selection, via second-order Akaike Information Criterions (AICc). The model that included individual identity and whether it was a morning or evening trial as fixed effects had the lowest AICc. (See supplementary text for details.)

Additional Terms in Model	AICc	ΔAICc
Trial, Date, Age, Morning/Evening	678.051	4.888
Date, Age, Morning/Evening	678.476	5.313
Trial, Age, Morning/Evening	675.756	2.593
Trial, Date, Morning/Evening	682.262	9.099
Trial, Date, Age	695.594	22.431
Date, Age	695.919	22.756
Date, Morning/Evening	677.736	4.573
Age, Morning/Evening	673.815	0.652
Trial, Age	691.239	18.076
Trial, Morning/Evening	677.604	4.441
Trial, Date	696.032	22.869
Date	692.378	19.215
Trial	691.757	18.594
Age	693.926	20.763
Morning/Evening	**673.163**	**0**
No additional terms	690.297	17.134

Table S10. We explored how PC1 of a novel object assay conducted on females was affected by individual identity, age, trial number (Trial), days since March 1st in which the trial started (Start Date), and whether the individual was subjected the novel object or baseline trial first (Novel Object/Baseline). We always retained individual identity in our models. For the other fixed effects, we conducted model selection, via second-order Akaike Information Criterions (AICc). The model that contained individual identity alone produced the best fit. (See supplementary text for details.)

Additional Terms in Model	AICc	ΔAICc
Trial, Start Date, Age, Novel Object/Baseline	544.301	16.862
Start Date, Age, Novel Object/Baseline	539.962	12.523
Trial, Age, Novel Object/Baseline	539.657	12.218
Trial, Start Date, Novel Object/Baseline	539.596	12.157
Trial, Start Date, Age	539.715	12.276
Start Date, Age	535.501	8.062
Start Date, Novel Object/Baseline	536.188	8.749
Age, Novel Object/Baseline	535.611	8.172
Trial, Age	535.193	7.754
Trial, Novel Object/Baseline	535.148	7.709
Trial, Start Date	535.127	7.688
Start Date	531.788	4.349
Trial	530.783	3.344
Age	531.247	3.808
Novel Object/Baseline	531.733	4.294
No additional terms	**527.439**	**0**

Table S11. We explored how PC1 of a novel object assay conducted on males was affected by individual identity, age, trial number (Trial), days since March 1st in which the trial started (Start Date), and whether the individual was subjected the novel object or baseline trial first (Novel Object/Baseline). We always retained individual identity in our models. For the other fixed effects, we conducted model selection, via second-order Akaike Information Criterions (AICc). The model that contained individual identity alone produced the best fit. (See supplementary text for details.)

Additional Terms in Model	AICc	ΔAICc
Trial, Start Date, Age, Novel Object/Baseline	775.270	16.31
Start Date, Age, Novel Object/Baseline	771.107	12.147
Trial, Age, Novel Object/Baseline	770.548	11.588
Trial, Start Date, Novel Object/Baseline	770.768	11.808
Trial, Start Date, Age	771.480	12.520
Start Date, Age	767.359	8.399
Start Date, Novel Object/Baseline	766.469	7.509
Age, Novel Object/Baseline	767.105	8.145
Trial, Age	766.838	7.878
Trial, Novel Object/Baseline	766.184	7.224
Trial, Start Date	767.039	8.079
Start Date	762.802	3.842
Trial	762.542	3.582
Age	763.446	4.486
Novel Object/Baseline	762.541	3.581
No additional terms	**758.960**	**0**

Chapter 4

Individual phenotypes shape the relationship between relative interspecific abundance and reproductive success of wild great tits (*Parus major*)

Individual phenotypes shape the relationship between relative interspecific abundance and reproductive success of wild great tits (*Parus major*)

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Keywords: personality, exploration behavior, age, social environment, spatial autocorrelation, heterospecific, competition

Abstract

Competition for limited resources is a fundamental ecological process in most natural systems and can drastically reduce individual fitness. The effects of intraspecific competition are typically stronger than the effects of interspecific competition, and therefore, given a fixed number of competitors in an individual's social environment, individuals may suffer smaller fitness declines in situations where a greater proportion of those competitors are heterospecifics, rather than conspecifics. Moreover, individuals with different phenotypes may be differentially affected by varying levels of competition, due to differences in competitive ability and/or differences in the way disparate phenotypes interact with their social environment. In this study, we used wild passerines to explore how the ratio of blue tit (*Cyanistes caeruleus*) to great tit (*Parus major*) neighbors (i.e. species composition) affects reproductive success in great tits. We further explored whether individual characteristics modulate the effects of species composition on reproductive success, specifically in terms of age and personality, as these traits have often been shown to relate to reproductive success in great tits. We found weak correlations between species composition and reproductive success. As the proportion of blue tit neighbors increased, there was a significant increase in the number of fledglings produced by great tits

and the proportion of the clutch fledged from a nest, but no effect on fledgling weight. The effect of species composition on the proportion of the clutch fledged varied depending on the age and personality type of the father, but not the mother. At higher levels of competition, older and/or faster exploring males fledged a lower proportion of their clutch than younger and/or slower exploring males, while at lower levels of competition, differences between ages and personality types vanished. Overall, our study suggests that, coupled with other selective forces, heterogeneity in an individual's social environment could potentially help maintain variation in male personality.

Introduction

Although social living can confer numerous benefits, such as reduced predation and enhanced access to social information (Alexander 1974; Altmann 1974; Wrangham 1979; Isbell 1994; Sterck et al. 1997; Rodman 1988), sociality also involves costs, particularly heightened competition for limited resources (Van Schaik et al. 1983; Janson 1988; Daviews et al. 1991; Côté & Poulinb 1995; Borries et al. 2008). Individuals may engage in contests for resources directly (i.e. interference competition), or they may compete indirectly, via depletion of scarce resources such as food or space (i.e. exploitative competition; Le Bourlot et al. 2014). Such competition often results in decreased survival and/or reproduction. Population density is often used as a measure of competitive pressure, with higher densities implying greater competition. Indeed, individuals often suffer reduced fitness at high population densities (i.e. negative density-dependence; Reiter et al. 1981; Alatalo & Lundberg 1984; Anderbrant et al.1985; Torok & Toth 1988; Perrins & McCleery 1989; Both 1998; Sillett et al. 2004).

Just as an individual may experience reduced fitness when competing with conspecifics, it may also suffer diminished fitness when competing with heterospecifics (e.g. Högstedt 1980; Yasuda 1990; Wilkin et al., 2006; Kuriwada et al. 2013; Harris & Siefferman 2014). Nevertheless, the effects of interspecific competition are typically weaker than the effects of intraspecific competition, given limited niche overlap with heterospecific competitors (Pianka 1974; Sale 1974; Connell 1983). Given this, when there are a fixed number of competitors in the local social environment, the effects of

competition may be weaker when there are lower ratios of conspecifics to heterospecifics. For example, in breeding birds that nest in close proximity, and under similar conditions, to heterospecifics, decreased competition resulting from higher proportions of heterospecific neighbors could increase reproductive success. Thus, in addition to examining competitor density, studying the relative ratios of conspecifics to heterospecifics in an organism's social environment provides an additional means to assessing the level of competitive pressure experienced by an individual.

Similar to the effects of one's social environment, an individual's own phenotype can have fitness consequences. For example, age and personality are two widely studied traits that have been linked to reproduction across a variety of species (Reiter et al. 1981; Berard 1999; East et al. 2003; Réale et al. 2009; Betini & Norris 2012; Mutzel et al. 2013; Vrublevska et al. 2015). In females, older individuals typically have higher reproductive success (Valdez 1976; Reiter et al. 1981; Sydeman et al. 1991; San José et al 1999), although many species also show reproductive senescence (Sherman 1976; Reid et al. 2003; Bouwhuis et al. 2009; 2010; Nussey et al. 2013). Similar linear (Sydeman et al. 1991; Lozano et al, 1996; Zedrosser et al. 2007) and negative quadratic (Berard 1999; East et al. 2003; Nussey et al. 2013) relationships have been observed for male age across species. Animal personality is defined as consistent between-individual differences in behavior (Dall et al. 2004; Sih et al. 2004; Bell et al. 2009). There is often a substantial genetic component to personality, and regular measures of personality include interindividual variation in exploration behavior, aggression, and boldness (reviewed in Dingemanse & Réale 2005). Like age, personality has been shown to affect reproductive success in several species (Réale et al. 2009; Betini & Norris 2012; Mutzel et al. 2013; Vrublevska et al. 2015). For example, in tree swallows (*Tachycineta bicolor*), male, but not female, aggression has been shown to predict fledging success, with more aggressive males fledging a higher number of offspring (Betini & Norris 2012). In blue tits (*Cyanistes caeruleus*), female, but not male, exploratory behavior may correlate with reproductive success, with faster exploring females fledging more offspring, likely due to higher rates of nestling feeding by faster explorers (Mutzel et al 2013).

It is important to note that individuals with different phenotypes, such as individuals of different age or personality, may be differentially affected by varying levels of competition (Clutton-Brock et al. 1987; Festa-Bianchet et al. 1998; Mysterud et al. 2001; Bonenfant et al. 2002; Cote et al. 2008; Le Galliard et al. 2015; Nicolaus et al. 2016). Increased levels of competition could create larger differences in fitness between individuals with dissimilar phenotypes (Clutton-Brock et al. 1987; Festa-Bianchet et al. 1998; Bonenfant et al. 2002). When competitive pressure increases, poorer quality individuals may experience greater declines in fitness than individuals of superior phenotypic quality that are better able to cope with increased competition. For instance, in the case of age, if older individuals were dominant over younger individuals (Reiter et al. 1981; Collis & Borgia 1992; Magaña et al. 2011), this may confer a competitive advantage to older individuals under higher competitive pressure. It could even be the case that older individuals benefit from increased experience compared to younger individuals, allowing the former to cope better with increased competition. In red deer (*Cervus elaphus*), increasing density, and thus presumably competition, increases differences in fecundity between young and old females and also between females that raised a calf through the summer prior and those that did not (Clutton-Brock et al. 1987). In contrast, heightened competition could instead work to reduce differences in fitness between individuals with different phenotypes (Clutton-Brock et al. 1987; Le Galliard et al. 2015). In common lizards (*Zootoca vivipara*), for example, less active individuals were found to have increased survival compared to more active individuals at low population densities, but there was no difference between phenotypes at medium or high population densities (Le Galliard et al. 2015). Lastly, it is possible that, certain phenotypes may actually be favored under high levels of competition, while others are favored under low levels of competition (Bonenfant et al. 2002; Cote et al. 2008; Nicolaus et al. 2016). For example, personality may affect the way an individual interacts with its environment, causing selection to favor individuals of one behavioral phenotype under high competition and individuals of the opposite behavioral phenotype under low competition (Cote et al. 2008; Nicolaus et al. 2016). In high density environments, more social juvenile common lizards have been found to survive better than less social

individuals, whereas in low density environments, less social lizards may survive better than more social individuals (Cote et al. 2008; but see Le Galliard et al. 2015). Although past work has focused on investigating differential fitness effects driven by fluctuating conspecific densities, it is also possible that individuals with different phenotypes may respond differently to variation in competition arising from changes in the ratios of competing conspecifics to heterospecifics. Because phenotypic variation may be maintained by variation in competitive pressure, studying how different phenotypes respond to variability in species composition may work to increase our understanding of the maintenance of phenotypic traits (Pruitt & Ferrari 2011).

Great tits (*Parus major*) and blue tits have been shown to compete for both food and nesting sites during the breeding season, and there is evidence to suggest that both intra- and interspecific competition negatively influence reproductive performance in great tits (Minot 1981; Minot & Perrins 1986; Wilkin et al. 2006; Dhondt 2012). On average, blue tits are subordinate to great tits; they are often outcompeted by great tits, and the effects of blue tits on great tit reproductive success may be weaker than that of conspecifics (Minot & Perrins 1986; Haftorn 1993; Hansen & Slagsvold 2004; Wilkin et al., 2006). Furthermore, past work has suggested great tits may perform better, in terms of the number of male recruits, when there are higher *versus* lower proportions of blue tits in their social environment (Dhondt 2012). In summary, it appears that competition with other great tits, as well as blue tits, reduces great tit reproductive success, but because blue tits impart smaller fitness declines to focal individuals than great tits, when the competitive environment is made up of a higher proportion of blue tits, great tits may experience fewer fitness declines than when faced with a higher proportion of conspecific competitors.

In addition to environmental effects, various measures of reproductive success have been shown to increase with both male and female age in great tits, with past studies showing a few of these measures declining in higher age classes in females, but not in males (Perrins 1965; Perrins & Moss 1974; Perrins & McCleery 1985; Bouwhuis et al. 2009; 2010). Furthermore, in great tits, older males may be more likely to attain dominance (although younger males may dominate older males if they

have the advantage of prior residency; Sandell & Smith 1991), and the higher social status enjoyed by older individuals may allow more senior age classes to suffer smaller declines in fitness with increases in competitive pressure, compared to younger individuals. Thus, heightened competition may increase fitness discrepancies between males of different age classes.

Like age, personality may affect reproductive success in great tits. In great tits, exploration behavior is a common measure of personality that is often used as a proxy for proactivity (Carere et al. 2005; Groothuis & Carere 2005; Quinn et al. 2009; Cole & Quinn 2012; Aplin 2013), as it correlates positively with both boldness and aggression (Verbeek et al. 1994; 1996; Gosling 2001). Exploration behavior may relate to increases in male fitness via increased extrapair paternity and/or more extrapair partners in slower exploring males (Araya-Ajoy et al. 2016; Abbey-Lee et al. 2018; but see Patrick et al. 2011; Roth et al. in press). Slower exploring females have been shown to have higher nest success, produce larger fledglings, and produce a higher number of recruits than faster explorers in a couple of studies (Both et al. 2005; Quinn et al. 2009), although Dingemanse et al. (2004) demonstrated that the relationship between female personality and number of recruits may fluctuate between years, with both faster and slower exploring mothers producing more recruits in years with high winter food abundance, and intermediate females producing more recruits in years with low winter food abundance.

In great tits, the exploration behavior of an individual may modulate the effects of competitive pressures on fitness. Nicolaus et al. (2016) have proposed that faster explorers may have higher fitness than slower explorers in highly competitive environments, as they may be better able to acquire resources due to positive correlations between exploration and dominance (Verbeek et al. 1996; Cole & Quinn 2012; but see Dingemanse & de Goede 2004 where the relationship is context specific in nonterritorial juveniles), while slower explorers may have higher fitness than faster explorers in less competitive environments, given lower energetic costs (Mathot et al. 2015; but see Bouwhuis et al. 2014). In partial support of this hypothesis, Quinn et al. (2009) found that, in some years in our study population, fecundity was negatively correlated to male exploration behavior in lower density areas,

but not in higher density areas. In contrast, Nicolaus et al. (2016) have also proposed that slower explorers may instead perform equally well across a range of competitive pressures, as they may handle environmental fluctuations better than faster explorers, allowing them to adapt to a range of competitive pressures (Verbeek et al. 1994; Nicolaus et al. 2016), while faster explorers may experience fitness declines with increased competition, as they may be less adept than slower explorers at managing social defeat (Verbeek et al. 1999; Carere et al. 2001; Nicolaus et al. 2016). Indeed, Nicolaus et al. (2016) demonstrated that faster exploring individuals had higher survival in lower *versus* higher density environments and had higher survival than slower explorers in lower density environments. Interestingly, however, Nicolaus et al. (2016) also found that slower explorers had higher survival in lower density conditions compared to higher density conditions and had higher survival than faster explorers in higher density environments. Combined, these results suggest poorer handling of social defeat by faster explorers, but it remains unclear why slower explorers experienced increased fitness with increased competition, rather than experiencing equal fitness across density gradients.

In this study, we used 14 years of breeding data to examine how great tit reproductive success is related to individual phenotypes (i.e. personality and age) and species composition (defined as the ratio of blue tit to great tit neighbors), and to ask whether the relationship between reproductive success and species composition differs based on phenotype. We first explored whether species composition was predicted by individual phenotypic traits. We then asked whether a relationship existed between species composition and measures of reproductive success (i.e. proportion of clutch that successfully fledged, number of fledglings, and fledgling weight). We also examined whether focal personality and age predicted reproductive success. Lastly, we explored if individuals with different phenotypes differed in their reproductive success under varying species composition. We predicted that, given superior quality, older individuals would have smaller declines in reproductive success with increasing competition (i.e. with decreasing proportions of blue tit neighbors) compared to younger individuals, creating larger fitness discrepancies between individuals of different ages with

increasing competitive pressure (Figure 1a). Regarding the differential effects of species composition on individuals with different personalities, we had two sets of mutually exclusive hypotheses. First, we predicted that, given tradeoffs between energetic requirements and resource acquisition, faster exploring individuals would enjoy increases in reproductive success with increasing competition, and slower explorers would exhibit the opposite pattern (Figure 1b). Conversely, we predicted that faster explorers would show decreases in reproductive success with increased competition, given poor handling of social defeat, while slower explorers would experience no significant change, as they may be better at buffering environmental variation (Figure 1c).

Methods

Study Population and Field Methods

Great tits and blue tits are hole nesting birds with predominantly socially monogamous mating systems (although blue tits can be polygynous in some parts of their range; Dhondt 1987a; 1987b). Every year for the last ca. 60 years, in Wytham Woods, Oxfordshire (51°46′ N, 1°20′ W), the identities of breeding males and females, clutch size, and fledgling success have been recorded using a standard methodology for great tits (Perrins 1965). All locally-born birds are ringed as nestlings. Immigrants (i.e. birds born outside Wytham) are ringed as juveniles or adults, during a large-scale ringing effort that occurs each winter (Voelkl et al. 2016), or at the nest during breeding season. Because the birth year is known, locally born birds can be assigned an exact age. For immigrant birds, plumage characteristics are used to determine whether an individual is in its first year of life or older (Svensson 1992). Immigrants caught with adult plumage are given an estimated age of 2 years (Bouwhuis et al. 2009), which is common in studies conducted on wild birds (e.g. Perreault et al. 1997; Lubjuhn et al. 2007). We only approximated 7.2 % of our total age data, which included data from all years within which an individual bred, and we approximated 5.5 % of ages for the individual birds used in our study (i.e. when each individual was only considered once).

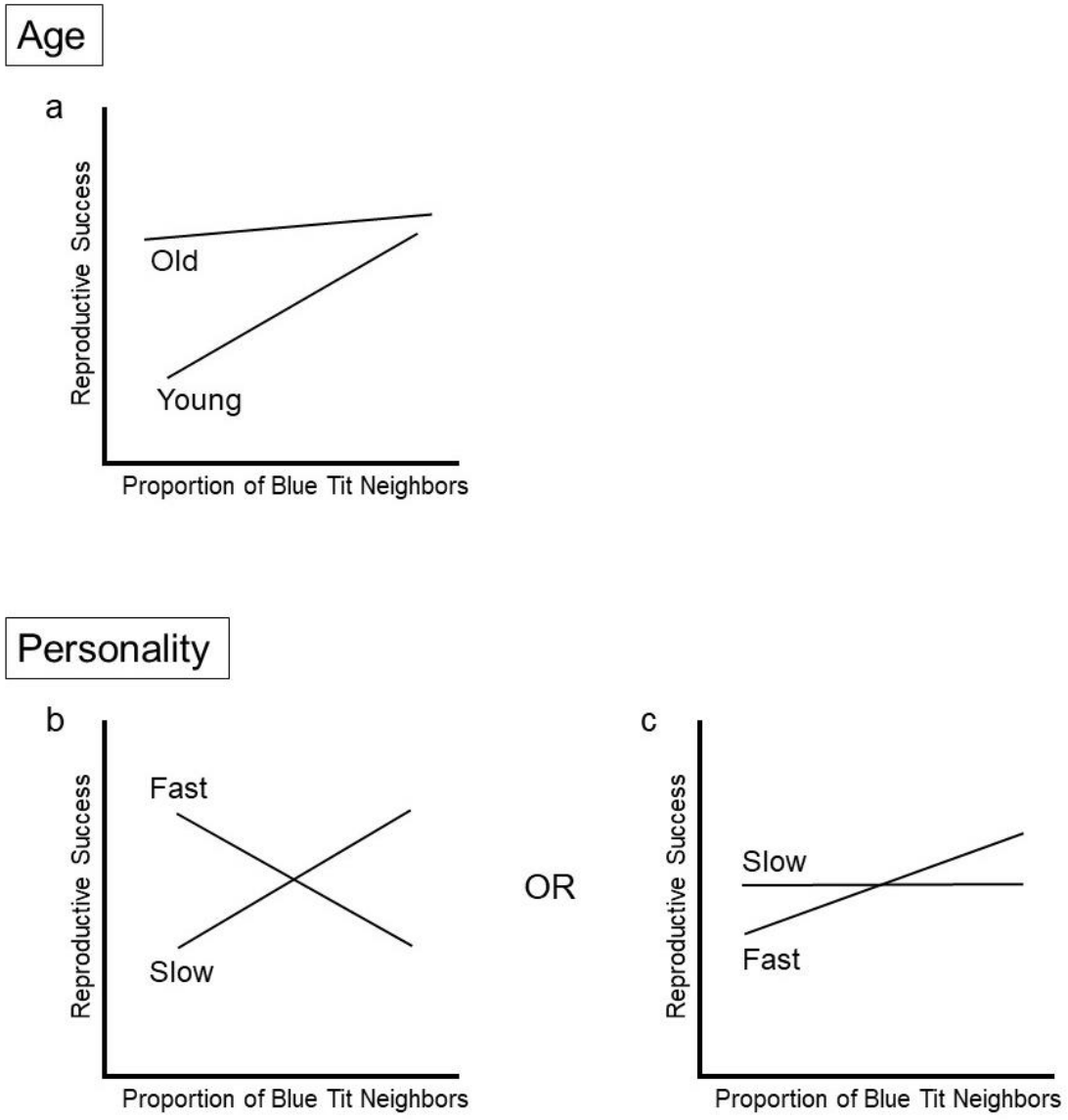

Figure 1. Predicted relationships between species composition (i.e. the proportion of blue tit neighbors) and reproductive success for old *versus* young individuals and fast *versus* slow personality types. We predicted that a) older individuals would, in general, have higher reproductive success than younger individuals, and we predicted that with increasing competition (i.e. decreasing proportions of blue tit neighbors), older individuals would suffer smaller declines in reproductive success compared to younger individuals. For personality, we had two mutually exclusive hypotheses. b) We predicted that when moving from high to low competition (i.e. increasing proportions of blue tit neighbors), faster exploring individuals would exhibit decreased reproductive success, while slower exploring individuals would experience increased reproductive success. c) We predicted that when moving from high to low competition, faster exploring individuals would have increased reproductive success, but slower exploring individuals would maintain similar levels of reproductive success along the competitive gradient.

Measuring Exploration Behavior

We conducted novel arena assays from 2005 - 2010 to test for interindividual variation in exploration behaviour, following the methods outlined in Quinn et al. (2009). These methods have been used regularly to study exploration behavior in this population (e.g. Quinn et al. 2011a; 2011b; Patrick et al. 2011; Aplin et al. 2013; 2014; Johnson et al. 2017; Firth et al. 2018; Roth et al. in press). Exploration behaviour is moderately repeatable and heritable in Wytham great tits (Quinn et al. 2009). Furthermore, in our population, exploration behavior has been shown to affect various processes including, but not limited to, male reproductive strategy (Patrick et al. 2011; Firth et al. 2018; but see Roth et al. in press), social network position (Aplin et al. 2013), foraging behavior (Quinn et al. 2011a), dispersal (Quinn et al. 2011b), and collective behavior (Aplin et al. 2014).

Statistical Methods

In Wytham Woods, great tits nest primarily in permanent nestboxes with known coordinates (N= 1015). In addition to nesting in great tit nestboxes, blue tits also nest in nestboxes specific to blue tits (i.e. boxes with a smaller entrance diameter that exclude great tits, N= 147 pre-2008; N = 187 from 2008 onwards), and natural cavities. Our study only considers focal great tits where all blue tit neighbors nested in great tit boxes, given a lack of equal opportunity for great tits and blue tits to nest in blue tit boxes. We further subset our data by removing the section of the woods named 'Extra' (Figure S1) because of the low density of nestboxes present in this section. Lachish et al. (2011) have demonstrated that low nestbox density is correlated with low blue tit recapture rates, suggesting that blue tits may be breeding in natural cavities in areas where there are low densities of nestboxes. By removing 'Extra', we attempt to limit sampling biases when calculating local species composition. Lastly, we removed two isolated great tit nestboxes from the bottom of a section of the woods known as 'Marley Plantation' (Figure S1), given the lack of neighboring nestboxes. We examined breeding tits from 2004 – 2017.

We used R 3.3.2 for all analyses (R Core Team 2018). We estimated territory boundaries using Voronoi polygons (i.e. polygons created around each occupied nestbox, enclosing the area closest to that nestbox relative to other nestboxes; Aurenhammer 1991). We defined neighbors as any great tit or blue tit breeding pair that shared a territory boundary with the focal pair, as such pairs should have the greatest influence on focal reproductive success, given that competition for food should be highest between pairs that share territory boundaries (Schlicht et al. 2014). For each breeding great tit pair, we ascertained local species composition by calculating the proportion of blue tit neighboring pairs. We controlled for local density, calculated here as the median log distance of great tit and blue tit neighbors, in our analyses, given that competition should be higher in areas of greater density. We also controlled for habitat quality and calculated habitat quality as the number of oak trees within a 75 m radius of the focal nest, as the caterpillars preferentially predated by tits are most commonly associated with oak foliage (Summerville et al. 2003; Wilkin et al. 2007; Wilkin & Sheldon 2009). We only included nests in our analyses where the identities of both parents were known, to eliminate the effects of potential single parent nests, as such nests are likely to have differential reproductive success due to the absence of one parent. However, because it was common for only one parent at each nest to have a known personality score, we tested males and females separately for all models. This prevented us from losing information about nests where both male and females had not been assayed for personality and allowed us to reduce nonindependence that may arise as a result of processes like assortative mating.

Because our analyses relied on the assumption that data points were independent, we needed to explore whether there was a tendency for any of our measured variables to clump together spatially (e.g. we examined if young individuals were more likely to breed in a certain area, while old individuals were more likely to breed in a separate area). We tested for spatial autocorrelation in the personalities and ages of breeding males and females using the ‘ape’ package to calculate Moran’s Indices for each of the aforementioned variables (Paradis & Schliep, 2018). We found limited

evidence of spatial autocorrelation (Table S1), and given this, we did not include a term for spatial autocorrelation in further models.

Predictors of Local Species Composition

To better understand the forces shaping an individual's local social environment, we examined whether the proportion of an individual's blue tit neighbors (i.e. local species composition) could be predicted by the focal individual's personality and age, in addition to the location of the focal nestbox (i.e. section of the woods), local density, and habitat quality. We ran generalized linear mixed models with a binomial family, with species composition as the response, and focal personality, focal age, section of the woods, local density, and habitat quality as fixed effects. Because our predictor variables had large differences in range, we scaled all fixed effects so that all predictor variables had a mean of zero and a standard deviation of 1. We included individual identity, nestbox, and year as random effects. We also calculated the repeatability of species (great tit *versus* blue tit) breeding in each nestbox from 2008-2017, using the rptBinary function in the rptR package (Nakagawa & Schielzeth 2010), to examine whether certain nestboxes were more likely to be used by great tits, compared to blue tits, and *vice versa*. For repeatability tests, we omitted data from 2004 – 2007 from our analyses, given that 40 additional blue tit boxes were added to the woods in 2008. There is probable cause to assume that this addition may have affected repeatability.

Predictors of Reproductive Success

We explored whether species composition, focal personality and focal age could predict reproductive success. We defined reproductive success as the proportion of the clutch that fledged, number of fledglings, and fledgling weight, running independent models for each response variable. Each measure gives a slightly different view of an individual's reproductive performance. The proportion of the clutch fledged gives insight into the percentage of a pair's initial investment that

came to fruition, number of fledglings provides information on the absolute reproductive output of a pair, and fledgling weight provides a measure of the quality of the fledged offspring.

For the proportion of the clutch that fledged, we ran generalized linear mixed models with a binomial family and included habitat quality, local density, lay date (number of days from April 1st in which the first egg was laid), species composition, focal personality, and focal age as fixed effects. A visual examination of the data distribution suggested evidence of a quadratic relationship between age and the observed measures of reproductive success for females, but not for males, which agrees with past work on Wytham tits (Perrins 1965; Perrins & Moss 1974; Perrins & McCleery 1985; Bouwhuis et al. 2009; 2010), and given this, we also included age^2 as a fixed effect in female models. We scaled all fixed effects and included focal identity, nestbox, year, and section of the woods as random effects. For models examining predictors of the number of fledglings, we ran similar models but used a zero inflated negative binomial family in place of the binomial family, given that there were a relatively high percentage of nests that did not fledge any chicks. For fledgling weight, we ran linear mixed models with individual fledgling weight as the response and species composition, focal age (and age^2 for female models), focal personality, habitat quality, local density, and lay date as fixed effects. We included focal identity, nestbox, year, and section of the woods as random effects. After exploring the effects of focal phenotype and species composition separately, we tested for interactions between species composition and focal phenotype. We ran the same models as above, but we included all two-way interactions between species composition and focal phenotype.

We found that the effects of non-focal predictors (i.e. those unrelated to focal phenotype – species composition, habitat quality, local density, and lay date) on reproductive success often differed between male and female models in significance, and occasionally, also in directionality (see Results; Tables 2 - 3 & S8). There are two reasons that such discrepancies may arise. First, such differences may occur because male models included a different subset of nests than female models. Second, male models included male age and male personality as fixed effects, while female models included female age and female personality as fixed effects. The inclusion of different fixed effects in male *versus*

female models may influence the effects of the various non-focal predictors on reproductive success, as different factors are being controlled for in each model type. We further investigated these potential underlying causes for the discrepancies between male and female models using a series of post hoc analyses. For each measure of reproductive success, we began by comparing a simplified male model to a simplified female model. Simplified male models were run on the same subset of data as the original male models, and were indeed identical to the original male models, with the exception that male age and male personality were no longer included as fixed effects and focal identity was no longer included as a random effect. Similarly, simplified female models were run on the same subset of data as the original female models and were indistinguishable from the original models, save for the fact that female age, female age^2, and female personality were no longer included as fixed effects and focal identity was no longer included as a random effect. A comparison of simplified male and female models allowed us to assess whether the discrepancies between the original male and female models resulted from 1) different subsets of nests being included in male and female models or 2) different fixed effects being included in each model. When the relationships between non-focal variables and reproductive success seen in the simplified male models paralleled the relationships observed in the simplified female models, we concluded that the initial discrepancies arose as a result of different fixed effects being included in male and female models. In contrast, if the relationships differed between the simplified male and female models, we concluded that the original discrepancies arose as a result of different subsets of nests being included in the original male and female models. Finally, to facilitate a deeper understanding of the overall effects of the observed non-focal variables on reproductive success throughout the woods, we examined models that included all great tit nests in our dataset, regardless of whether male or female phenotype was known. We ran a model for each measure of reproductive success that included species composition, habitat quality, local density, and lay date as fixed effects, and nestbox, year, and section of the woods as random effects. This allowed us to attain more accurate estimates of the effects of a focal nest's physical and social environment, as well as lay date, on reproductive success, using a larger dataset with less room for bias.

Results

A total of 2,001 focal great tit broods and 11,845 fledglings were observed in this study, with 91 to 222 breeding great tits per year over 14 years (mean ± SD = 142.929 ± 41.959). There was 59% overlap between male and female datasets for models examining the proportion of the clutch that fledged and the number of fledglings. There was 66% overlap between male and female datasets for models examining fledgling weight. Nestboxes were moderately repeatable in whether great tits or blue tits inhabited them across years (Repeatability ± SE = 0.139 ± 0.013, 95% CI = 0.103 - 0.153, $p < 0.001$).

Species Composition

We found that personality, age, and habitat quality did not predict an individual's proportion of blue tit neighbors for males or females (Table 1). We did, however, find that great tits had higher proportions of blue tit neighbors when local density was higher (i.e. when the median log distance of blue tit and great tit neighbors was lower; Table 1). Furthermore, some sections of the woods differed in the proportion of blue tit neighbors, when compared to the intercept, although the relevant sections differed between male and female models (Table 1).

Table 1. Effects of personality, age, habitat quality (i.e. Oaks within 75 m), local density (i.e. Median log Distance of Neighbors), and location in the woods (i.e. Section) on the proportion of blue tit neighbors in an individual's social environment. Intercept is 'Marley' (see Figure S1). The outputs for main effects are reported for models containing main effects only, whereas the outputs for two-way interactions are reported for models containing both main and interaction effects.

Predictor	Est. ± SE	z-value	p
Males (N = 570)			
Oaks within 75 m	0.003 ± 0.003	0.845	0.398
Median log Distance of Neighbors	-0.163 ± 0.046	-3.518	**<0.001**
Personality	0.002 ± 0.013	0.140	0.888
Age	-0.013 ± 0.030	-0.427	0.669
Section: Bean	-0.218 ± 0.163	-1.333	0.182
Section: Common Piece	-2.747 ± 1.036	-2.652	**0.008**
Section: Marley Plantation	-0.409 ± 0.110	-3.701	**<0.001**
Section: Broad Oak	-0.251 ± 0.142	-1.774	0.076
Section: Pasticks	-0.543 ± 0.474	-1.145	0.252
Section: Singing Way	-0.302 ± 0.160	-1.884	0.060
Section: Great Wood	-0.441 ± 0.136	-3.239	**0.001**
Females (N = 584)			
Oaks within 75 m	0.001 ± 0.003	0.208	0.835
Median log Distance of Neighbors	-0.104 ± 0.046	-2.260	**0.024**
Personality	-0.013 ± 0.012	-1.025	0.306
Age	-0.025 ± 0.034	-0.744	0.457
Section: Bean	-0.006 ± 0.164	-0.034	0.973
Section: Common Piece	-1.856 ± 1.110	-1.672	0.094
Section: Marley Plantation	-0.417 ± 0.115	-3.611	**<0.001**
Section: Broad Oak	-0.318 ± 0.150	-2.125	**0.034**
Section: Pasticks	-0.887 ± 0.730	-1.216	0.224
Section: Singing Way	-0.375 ± 0.155	-2.416	**0.016**
Section: Great Wood	-0.604 ± 0.136	-4.437	**<0.001**

Proportion of the Clutch that Fledged

When examining models that explored the main effects of species composition and focal phenotype, we found that very young and very old females fledged a lower proportion of their clutch than intermediately aged females (Est. ± SE = -0.177 ± 0.053; z-value = -3.351; p = 0.001; Table 2). Male phenotype had no effect on the proportion of the clutch that fledged (Table 2). In female models, April lay date had a significant effect on the proportion of the clutch that fledged, with a greater proportion fledged when clutches were laid earlier (Table 2). Although no relationship was seen between April lay date and the proportion of the clutch that fledged in male models, habitat quality and local density predicted the proportion of the clutch that fledged, with a greater proportion fledged when habitat quality was higher (i.e. when there were more oaks within a 75 m radius of a male's nest)

and when local density was lower (i.e. when the median log distance of neighbors was greater; Table 2). When we ran a post hoc analysis on models without focal phenotype, to examine why the relationships between non-focal predictors and reproductive success differed between male and female models, we found that simplified male and female models (i.e. models without fixed effects related to focal phenotype) agreed with respect to the effects of local density, but not with respect of the effects of habitat quality, April lay date, and species composition (Table S2). This suggests that the discrepancy between original male and female models with respect to local density arose as a result of different fixed effects being included in the original models, while the discrepancies between original male and female models with respect to habitat quality, April lay date, and species composition resulted from the inclusion of different subsets of nests in male and female models. Our final model that included all great tit nestboxes, regardless of whether male or female phenotype was known, suggested that, overall, pairs fledged a greater proportion of their clutch under lower local densities and when there was a higher proportion of blue tit neighbors (Table S2, Figure 2). Habitat quality and April lay date, on the other hand, had no effect on the proportion of the clutch that fledged (Table S2).

When examining interactions between focal phenotype and species composition, we found no evidence for any interaction between species composition and female age or personality. We did, however, find an interaction between age and species composition for males, in that males of different ages were more similar in the proportion of young fledged when they had a greater proportion of blue tit neighbors (Est. ± SE = 0.314 ± 0.094; z-value = 3.331; p = 0.001; Table 2; Figure 3a). We also found an interaction between male personality and species composition, in that males with different personalities fledged more similar proportions of their clutch when there were higher proportions of blue tit neighbors in their local social environment (Est. ± SE = 0.248 ± 0.096; z-value = 2.580; p = 0.010; Table 2; Figure 3b). Our interaction effects were dependent on the inclusion of random effects in our model, particularly father identity, nestbox identity, and section of the woods (Table S3).

Table 2. Effects of an individual's age and personality as well as habitat quality (i.e. Oaks within 75 m), local density (i.e. Median log distance of neighbors), April lay date, and the proportion of blue tit neighbors in the individual's local social environment (i.e. Proportion of BT) on the proportion of the clutch that fledged. The outputs for main effects are reported for models containing main effects only, whereas the outputs for two-way interactions are reported for models containing both main and interaction effects.

Predictor	Est. ± SE	z-value	p
Males (N = 570)			
Oaks within 75 m	0.468 ± 0.178	2.629	**0.009**
Median log Distance of Neighbors	0.291 ± 0.110	2.643	**0.008**
April Lay Date	-0.090 ± 0.088	-1.019	0.308
Proportion of BT	0.104 ± 0.093	1.117	0.264
Personality	0.046 ± 0.129	0.356	0.722
Age	-0.145 ± 0.088	-1.651	0.099
Proportion of BT * Personality	0.248 ± 0.096	2.580	**0.010**
Proportion of BT * Age	0.314 ± 0.094	3.331	**0.001**
Females (N = 584)			
Oaks within 75 m	0.015 ± 0.170	0.073	0.928
Median log Distance of Neighbors	-0.149 ± 0.121	-1.233	0.218
April Lay Date	-0.325 ± 0.113	-2.865	**0.004**
Proportion of BT	0.176 ± 0.097	1.816	0.069
Personality	0.251 ± 0.143	1.758	0.079
Age	-0.020 ± 0.119	-0.171	0.864
Age^2	-0.177 ± 0.053	-3.351	**0.001**
Proportion of BT * Personality	0.007 ± 0.098	-0.794	0.942
Proportion of BT * Age	0.103 ± 0.103	1.005	0.315
Proportion of BT * Age^2	0.002 ± 0.060	0.032	0.975

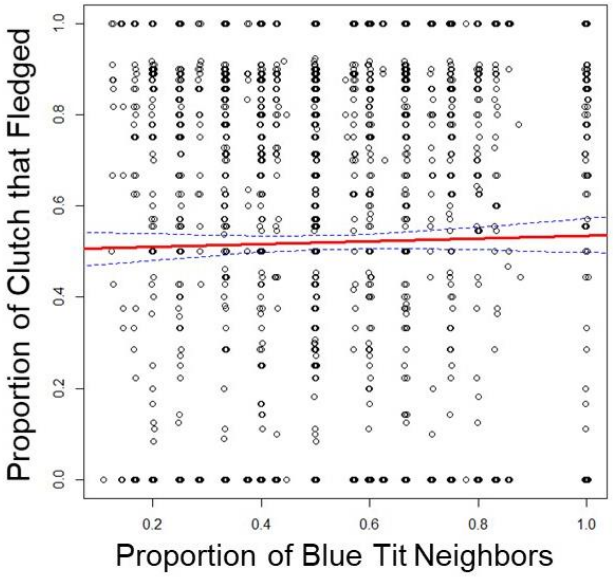

Figure 2. Weak relationship between a focal nest's proportion of blue tit neighbors and the proportion of the clutch that fledged.

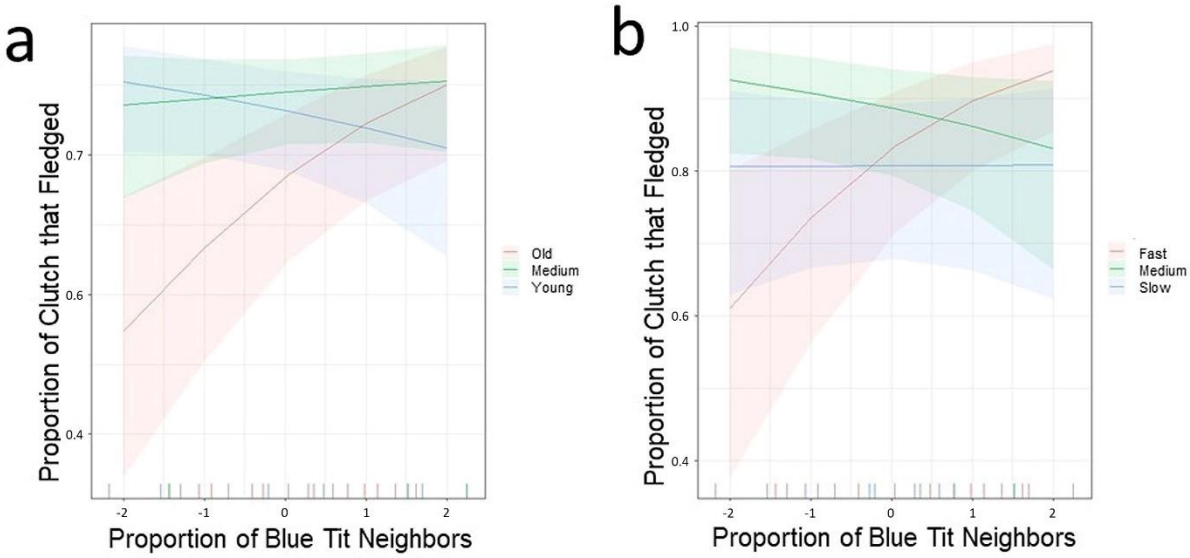

Figure 3. Effects of the interaction between focal phenotype and the proportion of blue tit neighbors on the proportion of the clutch that fledged for a) male age and b) male exploration behavior. As the proportion of blue tit neighbors increased, males of different ages and personalities became more similar in the proportion of their clutch fledged.

We conducted two sets of post hoc analyses to further explore the observed interactions between male phenotype and species composition. First, we divided our data at the median species composition, with one subset containing nests where there were low proportions of blue tit neighbors (335 nests) and the other subset containing nests where there were high proportions of blue tit neighbors (235 nests). We ran a generalized linear mixed model with a binomial family on each subsection of nests. We included the proportion of the clutch fledged as the response and focal age, focal personality, habitat quality, local density, and lay date as fixed effects. We scaled all fixed effects and included focal identity, nestbox, year, and section of the woods as random effects. We found a significant negative effect of age when the proportion of blue tit neighbors was low, but not when the proportion of blue tit neighbors was high (Table S4). In contrast to the effects of age, we did not find that male personality was a significant predictor of the proportion of the clutch fledged under any scenario (Table S4).

In the second set of post hoc analyses, we divided our data into three subsets containing young (1 year old), moderately aged (2 years old), and old males (≥ 3 years old). We also split our data into subsets based on personality, with three evenly distributed subsets containing fast, medium, and slow exploring males. Using the data subset based on age, we ran generalized linear mixed models with a binomial family on each of the three data subsets (young, moderately aged, and old). We included the proportion of the clutch fledged as the response and species composition, focal personality, habitat quality, local density, and lay date as fixed effects, and we scaled all fixed effects. We included focal identity, nestbox, year, and section of the woods as random effects. We found a significant positive correlation between species composition and the proportion of the clutch fledged for old, but not for young or moderately aged, males (Table S5). Similarly, using the data subset based on personality, we ran generalized linear mixed models with a binomial family for each personality category (fast, medium, slow), including the proportion of the clutch fledged as the response, and species composition, focal age, habitat quality, local density, and lay date as fixed effects. Again, we scaled all fixed effects. We included focal identity, nestbox, year, and section of the woods as random effects. Unlike age, we did not find a significant effect of species composition on the proportion of the clutch that fledged for fast, medium, or slow explorers (Table S6).

Number of Fledglings

Because the number of fledglings was strongly correlated to the proportion of the clutch fledged, for both male ($r = 0.907$, $p < 0.001$, $df = 569$) and female ($r = 0.905$, $p < 0.001$, $df = 582$) datasets, results for the number of fledglings can be found in the supplementary material.

Table 3. Effects of an individual's age and personality as well as habitat quality (i.e. Oaks within 75 m), local density (i.e. Median log distance of neighbors), April lay date, and the proportion of blue tit neighbors in the individual's local social environment (i.e. Proportion of BT) on fledgling weight. The outputs for main effects are reported for models containing main effects only, whereas the outputs for two-way interactions are reported for models containing both main and interaction effects.

Predictor	Est. ± SE	df	t-value	p
Males (N = 3712)				
Oaks within 75 m	0.026 ± 0.085	294.140	0.302	0.763
Median log Distance of Neighbors	-0.036 ± 0.060	611.447	-0.608	0.543
April Lay Date	-0.093 ± 0.044	1099.628	-2.123	**0.034**
Proportion of BT	-0.097 ± 0.044	1250.623	-2.209	**0.027**
Personality	-0.015 ± 0.065	272.828	-0.235	0.814
Age	-0.148 ± 0.048	507.465	-3.053	**0.002**
Proportion of BT * Personality	-0.077 ± 0.044	1022.576	-1.739	0.082
Proportion of BT * Age	-0.047 ± 0.042	2032.277	-1.115	0.265
Females (N = 3832)				
Oaks within 75 m	-0.009 ± 0.079	2.564e+02	-0.118	0.907
Median log Distance of Neighbors	-0.120 ± 0.056	9.392e+02	-2.157	**0.031**
April Lay Date	-0.165 ± 0.051	1.193e+03	-3.224	**0.001**
Proportion of BT	-0.131 ± 0.045	9.860e+02	-2.892	**0.004**
Personality	0.006 ± 0.068	2.446e+02	0.093	0.926
Age	-0.192 ± 0.053	8.428e+02	-3.586	**<0.001**
Age^2	0.016 ± 0.026	2.098e+03	0.616	0.538
Proportion of BT * Personality	-0.006 ± 0.044	1.012e+03	-0.148	0.882
Proportion of BT * Age	-0.035 ± 0.044	1.781e+03	-0.786	0.432
Proportion of BT * Age^2	0.040 ± 0.026	1.587e+03	1.538	0.124

Fledgling Weight

We found that younger males and younger females produced heavier fledglings (Males: Est. ± SE = -0.148 ± 0.048; df = 507.465; t-value = -3.053; p = 0.002; Females: Est. ± SE = -0.192 ± 0.053; df = 8.428e+02; t-value = -3.586; p < 0.001; Table 3). We also found that, in both male and female models, April lay date and species composition predicted fledgling weight, with heavier fledglings produced when clutches were laid earlier and when there were lower proportions of blue tit neighbors (Table 3). Additionally, in female, but not male, models, local density predicted fledgling weight, with heavier fledglings reared in lower density environments (i.e. when the median log distance of neighbors was greater). We explored the discrepancy between male and female models by rerunning models without focal phenotypes. There were no inconsistencies between simplified male and female models, suggesting that any discrepancies between male and female models were due to differences in which fixed effects were included in the model (Table S7). Lastly, when we examined the relationship

between non-focal variables and fledgling weight using the larger dataset that included all great tit nestboxes, regardless of whether focal phenotypes were known, we found that fledglings were significantly heavier when clutches were laid earlier (Table S7). Habitat quality, local density, and species composition did not predict fledgling weight. Furthermore, in our original models, there were no significant effects of the interaction between male or female age and personality on fledgling weight (Table 3).

Discussion

Using 14 years of breeding data from a wild population of great tits in Wytham Woods, UK, we found that male and female age, but not personality, predicted reproductive output. In contrast to past work on great tits (Perrins & McCleery 1985), we found that male age predicted fledgling weight, but not the proportion of the clutch that fledged or the number of fledglings produced, with younger males producing heavier offspring. This also contrasts with studies on other species demonstrating positive linear relationships (e.g. Sydeman et al. 1991; Lozano et al 1996; Zedrosser et al. 2007) or quadratic relationships (e.g. Berard 1999; East et al. 2003) between male age and reproductive success. Our finding that older males produced lighter offspring may reflect a decline in paternal investment with increased age. Furthermore, in line with past work on great tits (Perrins 1965; Perrins & Moss 1974; Perrins & McCleery 1985; Bouwhuis et al. 2009; 2010), and in line with past work in other species (e.g. Sherman 1976; Valdez 1976; Reiter et al. 1981; Sydeman et al. 1991; San José et al 1999; Reid et al. 2003), we found that female age predicted reproductive success. We found that very old and very young females fledged a smaller proportion of their clutch and produced fewer total fledglings. Our findings may reflect a lack of experience in very young females, and reproductive senescence in very old individuals (Reid et al. 2003). Furthermore, the decline in reproductive success at very old age could be a symptom of high mortality of individuals that invest heavily in reproduction (Reid et al. 2003). We also found a linear effect of female age on number of fledglings, in that older females produced more fledglings than younger individuals. Additionally, we found that older females

produced lighter fledglings. This may represent contrasting tradeoffs between quality and quantity of offspring, in younger *versus* older females, with younger females investing in fewer but heavier chicks and older females investing in more but lighter chicks. Tradeoffs between the size and number of offspring occur because parents must balance investment in provisioning current offspring with investment in creating additional offspring (Lack 1947; Stearns 1992; Roff 1992; 2002). Such tradeoffs are wide-ranging across species (e.g. Fleming & Gross 1990; Merilä & Wiggins 1995; Mappes & Koskela 2004; Walker et al. 2007), and past work has demonstrated negative correlations between nestling size and brood size in great tits (Smith et al. 1989). Our findings suggest that, in great tits, older and younger females may employ different routes to increasing reproductive success.

In addition to the effects of focal phenotype, we found that great tits fledged a higher proportion of their clutch and produced more fledglings when they had a higher proportion of blue tit neighbors. Although these relationships were very weak, they match past work suggesting that, while interspecific competition from blue tits can suppress reproductive success in great tits, the effects of interspecific composition on reproductive success are not as strong as the effects of intraspecific competition (Minot 1981; Wilkin et al. 2006; Dhondt 2012). Furthermore, previous studies indicate that male recruitment may be higher in great tits when there is a higher *versus* lower ratio of blue tits to great tits (Dhondt 2012). Although in the current study, the overall relationship between species composition and the proportion of clutch fledged was weak, we found that the strength of the effect of species composition varied depending on a male's phenotype.

We found an interaction between species composition and age, suggesting that relaxing competitive pressures (i.e. increasing proportions of blue tit neighbors) led males of different ages to converge in the proportion of their clutch fledged. Interestingly, however, 1) in more competitive environments, younger males had higher reproductive success than older males, and 2) older males experienced a decrease in reproductive success with increased competition, while younger birds did not. This contrasts with our original prediction that relaxed competition would allow males of different ages to converge in fitness by permitting younger males to increase their reproductive success to a

level similar to that of older males. We expected younger males would have lower reproductive success than older males in highly competitive environments, and we were surprised to find the opposite pattern. However, when there are higher proportions of great tit neighbors, intrusions by conspecific males should occur at relatively higher rates than in environments with lower proportions of conspecific neighbors. Older males may hold higher quality territories than younger males (Dhondt 1971); thus, they may suffer disproportionately higher intrusion rates than younger males when there are higher proportions of great tit neighbors in their local social environment. It seems possible that under such conditions, older males spend more time defending their superior territory than younger individuals, resulting in decreased paternal investment and reducing the proportion of the clutch that fledges. In environments with low proportions of great tit neighbors, males of all ages may spend little time on territory defense, allowing more time for parental care across the board. We further explored this possibility by running a post hoc test to examine whether older males had higher quality territories. A generalized liner mixed model with a Poisson family that included habitat quality (i.e. number of oak trees within a 75 m radius of the focal nest) as the response, male age as a fixed effect, and focal identity, nestbox, year, and section of the woods as random effects did not suggest an effect of male age on habitat quality (Est. ± SE = -0.001 ± 0.012, z-value = -0.068, p = 0.904). Given such, it remains unclear why older males had lower reproductive success than younger males in highly competitive environments.

Work in other species has also demonstrated that competitive pressure may have differential fitness effects on differently aged individuals. In red deer, the difference in fecundity between young and old hinds and between hinds that reared a calf through the previous summer and hinds that did not, was found to increase with increasing density (Clutton-Brock et al. 1987). Contrary to our findings, however, younger deer appeared to experience a greater decline in reproductive success with increased competition compared to older females (Clutton-Brock et al. 1987). Similarly, in red deer, the pregnancy rate of yearlings may be lower at higher *versus* lower densities, while the pregnancy rate of adults may remain stable across variation in density (Bonenfant et al. 2002). Density and age may also

interact to affect male, but not female, survival in red deer (Bonenfant et al. 2002). When given three age classes: young, prime (i.e. intermediately aged males who are in their prime breeding years), and old, young and old males were found to enjoy higher survival in low density environments compared to high density environments (Bonenfant et al. 2002). Interestingly, prime aged stags were found to have better survival under high density compared to low density conditions (Bonenfant et al. 2002).

In addition to the interaction between species composition and age, we found an interaction between species composition and male personality, which suggested that relaxed competitive pressure allowed males of different personalities to converge in the proportion of their clutch fledged. Other studies have also reported interactions between competition and personality. Somewhat in contrast to our findings, Quinn et al. (2009) found evidence that, in some years, fecundity was negatively correlated to male exploration behavior in lower density areas (i.e. under low competition), but not in higher density areas in Wytham great tits. Although Nicolaus et al. (2016) found no evidence to suggest an interaction between exploration behavior and density on the number of recruits (i.e. fecundity selection) in a Dutch population of great tits, the authors found that faster exploring individuals survived better than slower explorers in low density environments and *vice versa* (Nicolaus et al. 2016). They also found that faster explorers had higher survival in low density environments compared to high density environments, while slow exploring individuals were found to exhibit the opposite pattern (Nicolaus et al. 2016). Both the findings in our study as well as those in Nicolaus et al. (2016) may arise as a result of faster exploring great tits responding poorly to social defeat (Verbeek et al. 1999; Carere et al. 2001; Nicolaus et al. 2016). Furthermore, our results may indicate that slower exploring males are better able to buffer changes in their social environment compared to faster exploring males (Verbeek et al. 1994).

Effects of interactions between personality and competition pressure on fitness have also been found in species other than great tits. In one study, common lizards with different levels of sociality or boldness were not found to exhibit differences in reproductive success at different conspecific densities (Cote et al. 2008). However, in this study, sociality, but not boldness, was found to interact

with density to affect survival (Cote et al. 2008). More social individuals survived better than less social individuals in higher density conditions, while less social individuals survived better than more social individuals in lower density conditions (Cote et al. 2008). Interestingly, a second study conducted on this species found no interaction between density and sociality (or boldness) on survival, but the authors did find a marginally nonsignificant trend, suggesting that breeding frequency was higher in more *versus* less social lizards at lower densities, and higher in less *versus* more social lizards at higher densities (Le Galliard et al. 2015). Furthermore, at lower densities, less active individuals survived better than more active individuals, while no relationship between activity and survival was seen at higher densities (Le Galliard et al. 2015). Similarly, Harris & Siefferman (2014) found that while pairs of Eastern bluebirds (*Sialia sialis*) raised lighter nestlings in areas of higher *versus* lower interspecific competition with tree swallows (*Tachycineta bicolor*), pairs that mated assortatively at both extremes of the aggression spectrum produced heavier fledglings that other pair combinations, in areas with higher interspecific competition (Harris & Siefferman 2014). In areas with lower interspecific competition, there was no effect of assortativity on fledgling weight (Harris & Siefferman 2014). Furthermore, there were no significant effects of interactions between competition and aggression on the number of chicks fledged (Harris & Siefferman 2014).

It should be noted that local density appeared to be more important than species composition in predicting the proportion of the clutch fledged in our study, suggesting that absolute interspecific abundance had a stronger effect than relative interspecific abundance. Given this, it is possible that the differential effects of species composition on individuals possessing different phenotypes may be outweighed by differential effects of local density, but we did not examine this possibility in the current study. Although the effect of an interaction between density and personality on reproductive performance has been examined on our population previously (Quinn et al., 2009), the effect of an interaction between density and age has not, and we suggest that future work be conducted to explore this possibility. In a similar vein, however, we found that the species composition of one's breeding environment was predicted by local density, with great tits having a higher proportion of blue tit

neighbors in higher density conditions. Two potential explanations for this pattern are as follows. First, blue tits may be more likely to nest in natural cavities in areas where there is a lower density of provided nestboxes, and more likely to nest in nestboxes in locations where there is a higher density of provided nestboxes (Lachish et al. 2011), causing great tits to appear to have higher proportions of blue tit neighbors in higher density areas. Second, the provided nestboxes are not evenly spaced throughout our study site, and areas containing a higher density of provided nestboxes may being less preferred breeding sites than areas containing a lower density of provided nestboxes, due to spatial constraints causing increased competition (Reiter et al. 1981; Alatalo & Lundberg 1984; Anderbrant et al.1985; Torok & Toth 1988; Sillett et al. 2004). Because blue tits are subordinate to great tits (Haftorn 1993; Hansen & Slagsvold 2004), they may be forced to nest in inferior locations (Minot & Perrins 1986), resulting in higher proportions of blue tits in areas with a higher density of provided nestboxes. If blue tits are confined to nesting in poorer quality nestboxes, while great tits monopolize higher quality sites, this may also explain the moderate repeatability we observed in which of the two species nested in each nestbox across years.

Lastly, it is important to mention that, in our study, models run on subsets where male phenotypes were known differed from models run on subsets where female phenotypes were known in whether non-focal variables influenced the proportion of the clutch fledged, even when focal phenotypes were not considered in the models. This suggests that different subsets of nests produced different patterns, which is surprising given our reasonably large sample sizes, as one might assume less bias with larger sample sizes. Such patterns would be generated if males were more likely to be of known age and personality for certain nestboxes and females were more likely to be of known age and personality for other nestboxes, and such patterns may be indicative of sex-specific trapping and/or sampling biases occurring at a local scale. Future work is needed to examine the underlying mechanisms of these biases.

In conclusion, competition may be relaxed with increasing ratios of blue tits to great tits in a great tits' local social environment, allowing a slight overall increase in great tit reproductive success.

Importantly, however, our results suggest that the effect of species composition does not affect individual male phenotypes equally, with relaxed competition reducing differences in reproductive success between older and younger males and between faster and slower exploring males. Given this, heterogeneity in one's social environment may have important implications for the maintenance of variation in personality, especially when paired with other selective forces, and future studies should consider this possibility.

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Supplementary Information

Number of Fledglings

We found a quadratic effect of female age in that very young and very old females produced fewer total fledglings than intermediately aged females (Est. ± SE = -0.061 ± 0.018; z-value = -3.449; p = 0.001; Table S8). There was also a linear effect of age, suggesting that older females produced more fledglings (Est. ± SE = 0.061 ± 0.029; z-value = 2.130; p = 0.033; Table S8). Male age and male and female personality had no effect on the number of fledglings reared (Table S8). In both male and female models, April lay date predicted the number of fledglings, with more fledglings produced when clutches were laid earlier (Table S8). In male, but not female, models, habitat quality also had a significant effect on the number of fledglings, with more fledglings reared when there were more oak trees within a 75 m radius of a male's nest (Table S8). In contrast to the original models, our post hoc test conducted to explore the cause of these discrepancies yielded no differences between the simplified male and female models, suggesting that differences arose between the original models given the inclusion of different fixed effects (Table S9). Finally, when we used a larger dataset that included all great tit nestboxes, irrespective of whether ages or personalities of breeding birds were known, to examine the relationships between non-focal variables and number of fledglings, we found that while habitat quality did not predict the number of fledglings, more fledglings were produced when great tits had a higher proportion of blue tit neighbors, when clutches were laid earlier, and when local density was lower (Table S9; Figure S2). We found no evidence that any interactions between male or female focal phenotypes and species composition predicted the number of fledglings reared.

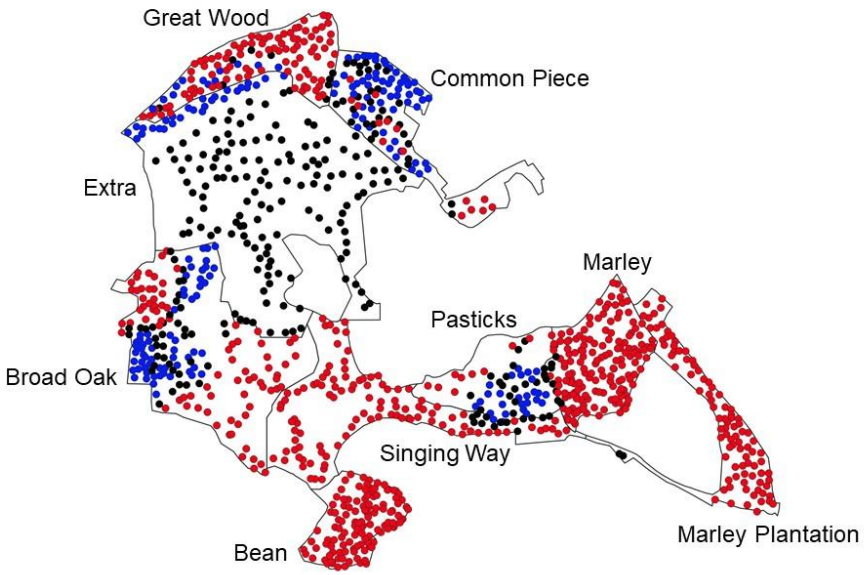

Figure S1. Map of Wytham Woods. Red dots represent great tit nestboxes that were used in our study, black dots represent great tit nestboxes that were not used in our study, and blue dots represent blue tit nestboxes. 40 of the pictured blue tit boxes were added to the woods in 2008.

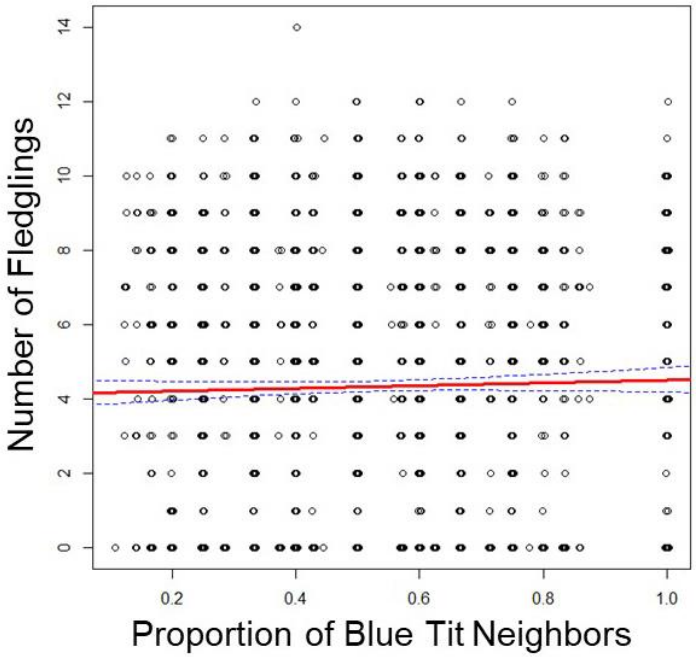

Figure S2. Weak relationship between a focal nest's proportion of blue tit neighbors and the number of fledglings produced.

Table S1. Observed Moran's Indices (Moran's I) for female and male age and personality from 2004-2017. Boldface values represent significant effects. "NA" indicates that there was not enough data to accurately calculate Moran's I.

Year	♂ Age	♀ Age	♂ Personality	♀ Personality
2004 Moran's I	-0.015	0.015	-0.018	0.064
2005 Moran's I	-0.018	-0.004	0.037	0.042
2006 Moran's I	-0.005	-0.010	0.011	**0.052**
2007 Moran's I	0.016	0.018	-0.018	-0.015
2008 Moran's I	**0.043**	0.003	0.020	-0.025
2009 Moran's I	0.013	-0.019	0.024	-0.049
2010 Moran's I	-0.004	-0.007	0.009	0.017
2011 Moran's I	-0.029	-0.023	0.211	-0.120
2012 Moran's I	0.017	-0.013	-0.068	-0.128
2013 Moran's I	**0.082**	-0.013	-0.072	-0.123
2014 Moran's I	0.010	-0.010	-0.109	-0.057
2015 Moran's I	**0.037**	0.006	0.041	-0.054
2016 Moran's I	-0.013	0.021	NA	NA
2017 Moran's I	0.005	-0.012	NA	NA

Table S2. Effects of habitat quality (i.e. Oaks within 75 m), local density (i.e. Median log Distance of Neighbors), April lay date, and the proportion of blue tit neighbors (i.e. Proportion of BT) on the proportion of the clutch that fledged for a) a subset of the data in which male age and personality were known, b) a subset of the data in which female age and personality were known, and c) a dataset that included all great tit nestboxes, regardless of whether focal phenotypes were known.

Predictor	Est. ± SE	z-value	p
Subset Male Phenotype Known (N = 570)			
Oaks within 75 m	0.420 ± 0.127	3.285	**0.001**
Median log Distance of Neighbors	0.320 ± 0.083	3.878	**<0.001**
April Lay Date	-0.095 ± 0.067	-1.414	0.157
Proportion of BT	0.110 ± 0.062	1.785	0.074
Subset Female Phenotype Known (N = 584)			
Oaks within 75 m	-0.006 ± 0.118	-0.050	0.960
Median log Distance of Neighbors	0.169 ± 0.082	2.061	**0.039**
April Lay Date	-0.374 ± 0.076	-4.953	**<0.001**
Proportion of BT	0.297 ± 0.060	4.931	**<0.001**
Full Data (N = 2001)			
Oaks within 75 m	0.019 ± 0.060	0.320	0.749
Median log Distance of Neighbors	0.218 ± 0.036	6.107	**<0.001**
April Lay Date	-0.018 ± 0.030	-0.591	0.555
Proportion of BT	0.063 ± 0.026	2.452	**0.014**

Table S3. The significance of the interaction between male personality and species composition (i.e. Proportion of BT * Personality) and the interaction between male age and species composition (i.e. Proportion of BT * Age) was dependent on the inclusion of nestbox identity, father identity, section of the woods, and/or year as random effects in our model. Here we list the outputs for the interactions terms from post hoc models where some or all of these random effects were not included.

Predictor	Est. ± SE	z-value	p
All Random Effects			
Proportion of BT * Personality	0.248 ± 0.096	2.580	**0.010**
Proportion of BT * Age	0.314 ± 0.094	3.331	**0.001**
Father, Section, Year			
Proportion of BT * Personality	0.012 ± 0.065	0.184	0.854
Proportion of BT * Age	0.307 ± 0.067	4.609	**<0.001**
Nestbox, Section, Year			
Proportion of BT * Personality	0.084 ± 0.059	1.419	0.156
Proportion of BT * Age	0.280 ± 0.066	4.259	**<0.001**
Father, Nestbox, Year			
Proportion of BT * Personality	0.257 ± 0.097	2.657	**0.008**
Proportion of BT * Age	0.314 ± 0.094	3.328	**0.001**
Father, Nestbox, Section			
Proportion of BT * Personality	0.266 ± 0.094	2.828	**0.005**
Proportion of BT * Age	0.242 ± 0.089	2.730	**0.006**
Father & Nestbox			
Proportion of BT * Personality	0.274 ± 0.094	2.909	**0.004**
Proportion of BT * Age	0.244 ± 0.089	2.747	**0.006**
Father & Section			
Proportion of BT * Personality	0.028 ± 0.063	0.441	0.659
Proportion of BT * Age	0.221 ± 0.062	3.554	**<0.001**
Father & Year			
Proportion of BT * Personality	0.021 ± 0.065	0.318	0.750
Proportion of BT * Age	0.317 ± 0.067	4.739	**<0.001**
Nestbox & Section			
Proportion of BT * Personality	0.092 ± 0.057	1.608	0.108
Proportion of BT * Age	0.193 ± 0.061	3.150	**0.002**
Nestbox & Year			
Proportion of BT * Personality	0.081 ± 0.059	1.363	0.173
Proportion of BT * Age	0.276 ± 0.066	4.202	**<0.001**
Section, Year			
Proportion of BT * Personality	0.011 ± 0.036	0.307	0.759
Proportion of BT * Age	0.105 ± 0.040	2.622	**0.009**
Father			
Proportion of BT * Personality	0.040 ± 0.065	0.621	0.535
Proportion of BT * Age	0.230 ± 0.063	3.632	**<0.001**
Nestbox			
Proportion of BT * Personality	0.091 ± 0.059	1.557	0.119
Proportion of BT * Age	0.190 ± 0.063	3.026	**0.002**
Section			
Proportion of BT * Personality	0.020 ± 0.035	0.553	0.580
Proportion of BT * Age	0.060 ± 0.039	1.536	0.125
Year			
Proportion of BT * Personality	0.003 ± 0.035	0.097	0.922
Proportion of BT * Age	0.084 ± 0.038	2.180	**0.029**
No Random Effects			
Proportion of BT * Personality	0.008 ± 0.034	0.243	0.808
Proportion of BT * Age	0.037 ± 0.037	1.000	0.317

Table S4. Effects of a male's age and personality as well as habitat quality (i.e. Oaks within 75 m), local density (i.e. Median log distance of neighbors), and April lay date on the proportion of the clutch that fledged for nests with low proportions of blue tit neighbors (Low Proportion of BT) and nests with high proportions of blue tit neighbors (High Proportion of BT).

Predictor	Est. ± SE	z-value	p
Low Proportion of BT (N = 335)			
Oaks within 75 m	0.350 ± 0.187	1.875	0.061
Median log Distance of Neighbors	0.158 ± 0.134	1.184	0.237
April Lay Date	0.132 ± 0.120	1.102	0.271
Personality	-0.073 ± 0.140	-0.519	0.604
Age	-0.249 ± 0.113	-2.207	**0.027**
High Proportion of BT (N = 235)			
Oaks within 75 m	0.826 ± 0.278	2.974	**0.003**
Median log Distance of Neighbors	0.444 ± 0.227	1.959	0.050
April Lay Date	-0.387 ± 0.190	-2.041	**0.041**
Personality	0.288 ± 0.230	1.251	0.211
Age	0.055 ± 0.187	0.294	0.768

Table S5. Effects of the proportion of blue tit neighbors in the individual's local social environment (i.e. Proportion of BT), habitat quality (i.e. Oaks within 75 m), local density (i.e. Median log distance of neighbors), April lay date, and focal male personality on the proportion of the clutch that fledged for young, moderately aged, and old males.

Predictor	Est. ± SE	z-value	p
Young (N = 249)			
Oaks within 75 m	0.360 ± 0.221	1.632	0.103
Median log Distance of Neighbors	-0.002 ± 0.195	-0.010	0.992
April Lay Date	0.106 ± 0.184	0.576	0.565
Proportion of BT	0.011 ± 0.181	0.061	0.951
Personality	0.189 ± 0.164	1.153	0.249
Moderately Aged (N = 150)			
Oaks within 75 m	0.571 ± 0.228	2.501	**0.012**
Median log Distance of Neighbors	0.033 ± 0.226	0.145	0.885
April Lay Date	-0.346 ± 0.226	-1.531	0.126
Proportion of BT	0.042 ± 0.221	-0.191	0.848
Personality	0.307 ± 0.225	1.367	0.171
Old (N = 171)			
Oaks within 75 m	1.120 ± 0.411	2.727	**0.006**
Median log Distance of Neighbors	0.877 ± 0.249	3.519	**<0.001**
April Lay Date	-0.207 ± 0.186	-1.115	0.265
Proportion of BT	0.492 ± 0.250	1.970	**0.049**
Personality	-0.151 ± 0.314	-0.481	0.631

Table S6. Effects of the proportion of blue tit neighbors in the individual's local social environment (i.e. Proportion of BT), habitat quality (i.e. Oaks within 75 m), local density (i.e. Median log distance of neighbors), April lay date, and focal male age on the proportion of the clutch that fledged for slow exploring, moderately exploring, and fast exploring males.

Predictor	Est. ± SE	z-value	p
Slow Exploring (N = 192)			
Oaks within 75 m	0.775 ± 0.263	2.951	**0.003**
Median log Distance of Neighbors	0.459 ± 0.195	2.359	**0.018**
April Lay Date	0.176 ± 0.163	1.083	0.279
Proportion of BT	0.138 ± 0.181	0.765	0.444
Age	-0.346 ± 0.175	-1.983	**0.047**
Moderately Exploring (N = 188)			
Oaks within 75 m	0.529 ± 0.330	1.601	0.109
Median log Distance of Neighbors	0.370 ± 0.235	1.577	0.115
April Lay Date	-0.433 ± 0.198	-2.185	**0.029**
Proportion of BT	-0.199 ± 0.190	-1.045	0.296
Age	0.127 ± 0.194	0.656	0.512
Fast Exploring (N = 190)			
Oaks within 75 m	0.507 ± 0.335	1.515	0.130
Median log Distance of Neighbors	0.021 ± 0.247	0.085	0.932
April Lay Date	0.446 ± 0.254	1.753	0.080
Proportion of BT	0.305 ± 0.192	1.586	0.113
Age	-0.255 ± 0.194	-1.318	0.188

Table S7. Effects of habitat quality (i.e. Oaks within 75 m), local density (i.e. Median log Distance of Neighbors), April lay date, and the proportion of blue tit neighbors (i.e. Proportion of BT) on fledgling weight for a) a subset of the data in which male age and personality were known, b) a subset of the data in which female age and personality were known, and c) a dataset that included all great tit nestboxes, regardless of whether focal phenotypes were known.

Predictor	Est. ± SE	df	t-value	p
Subset Male Phenotype Known (N = 3712)				
Oaks within 75 m	0.026 ± 0.074	276.884	0.350	0.727
Median log Distance of Neighbors	-0.029 ± 0.057	945.102	-0.504	0.615
April Lay Date	-0.070 ± 0.042	2175.263	-1.678	0.093
Proportion of BT	-0.055 ± 0.037	2786.202	-1.497	0.135
Subset Female Phenotype Known (N = 3832)				
Oaks within 75 m	-0.045 ± 0.067	257.885	-0.668	0.504
Median log Distance of Neighbors	-0.047 ± 0.045	1571.267	-1.031	0.303
April Lay Date	0.020 ± 0.040	2377.878	0.510	0.610
Proportion of BT	0.023 ± 0.032	3150.531	0.724	0.469
Full Data (N = 11845)				
Oaks within 75 m	0.013 ± 0.043	5.175e+02	0.285	0.776
Median log Distance of Neighbors	0.046 ± 0.026	5.826e+03	1.778	0.076
April Lay Date	-0.063 ± 0.020	1.103e+04	-3.095	**0.002**
Proportion of BT	0.027 ± 0.018	1.110e+04	1.502	0.133

Table S8. Effects of an individual's age and personality as well as habitat quality (i.e. Oaks within 75 m), local density (i.e. Median log distance of neighbors), April lay date, and the proportion of blue tit neighbors in the individual's local social environment (i.e. Proportion of BT) on number of fledglings. The outputs for main effects are reported for models containing main effects only, whereas the outputs for two-way interactions are reported for models containing both main and interaction effects.

Predictor	Est. ± SE	z-value	p
Males (N = 570)			
Oaks within 75 m	0.057 ± 0.024	2.421	**0.015**
Median log Distance of Neighbors	0.044 ± 0.023	1.860	0.063
April Lay Date	-0.090 ± 0.025	-3.596	**<0.001**
Proportion of BT	0.019 ± 0.022	0.885	0.376
Personality	0.024 ± 0.021	1.150	0.250
Age	-0.028 ± 0.022	-1.284	0.199
Proportion of BT * Personality	0.006 ± 0.021	0.287	0.774
Proportion of BT * Age	0.019 ± 0.023	0.791	0.429
Females (N = 584)			
Oaks within 75 m	0.010 ± 0.024	0.418	0.676
Median log Distance of Neighbors	0.045 ± 0.024	1.922	0.055
April Lay Date	-0.135 ± 0.027	-4.917	**<0.001**
Proportion of BT	0.016 ± 0.022	0.716	0.474
Personality	0.010 ± 0.022	0.468	0.640
Age	0.061 ± 0.029	2.130	**0.033**
Age^2	-0.061 ± 0.018	-3.449	**0.001**
Proportion of BT * Personality	-0.029 ± 0.021	-1.406	0.160
Proportion of BT * Age	0.001 ± 0.028	0.045	0.943
Proportion of BT * Age^2	-0.011 ± 0.019	-0.588	0.557

Table S9. Effects of habitat quality (i.e. Oaks within 75 m), local density (i.e. Median log Distance of Neighbors), April lay date, and the proportion of blue tit neighbors (i.e. Proportion of BT) on the number of fledglings for a) a subset of the data in which male age and personality were known, b) a subset of the data in which female age and personality were known, and c) a dataset that included all great tit nestboxes, regardless of whether focal phenotypes were known.

Predictor	Est. ± SE	z-value	p
Subset Male Phenotype Known (N = 570)			
Oaks within 75 m	0.057 ± 0.024	2.410	0.015
Median log Distance of Neighbors	0.043 ± 0.024	1.812	0.070
April Lay Date	-0.088 ± 0.025	-3.514	**<0.001**
Proportion of BT	0.020 ± 0.022	0.912	0.362
Subset Female Phenotype Known (N = 584)			
Oaks within 75 m	0.007 ± 0.024	0.283	0.777
Median log Distance of Neighbors	0.039 ± 0.024	1.631	0.103
April Lay Date	-0.143 ± 0.027	-5.223	**<0.001**
Proportion of BT	0.016 ± 0.022	0.741	0.459
Full Data (N = 2001)			
Oaks within 75 m	0.001 ± 0.015	0.042	0.966
Median log Distance of Neighbors	0.054 ± 0.015	3.645	**<0.001**
April Lay Date	-0.083 ± 0.017	-4.949	**<0.001**
Proportion of BT	0.036 ± 0.014	2.661	**<0.001**

Chapter 5

Group personality composition predicts emergent group-level social patterns and structure in red junglefowl (*Gallus gallus*)

Group personality composition predicts emergent group-level social patterns and structure in red junglefowl (*Gallus gallus*)

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Abstract

Social living is ubiquitous across species, and patterns of sociality are regulated by associated fitness costs and benefits, such as food depletion or predator protection. Because differences in within individual behavioural consistencies across individuals (i.e. personality) can modulate social interactions among group members, the personality composition of a group is expected to influence costs and benefits of sociality, shaping social patterns and structure. However, few studies have experimentally explored this expectation. Using replicate groups of 12 red junglefowl (*Gallus gallus*) with different sex ratios, we explored the effects of group personality composition on emergent group-level social dynamics. Specifically, we examined the effects of mean exploration and mean boldness of same-sex group members on the frequency and network structure of different types of social interactions: male sexual harassment of females, intrasexual aggression, and intra- and intersexual allopreening. We also explored how group personality composition affected the linearity and steepness of same-sex social hierarchies. Male group exploration predicted patterns of sexual harassment as well as female-female aggression and allopreening, whilst male group boldness explained patterns of female-female aggression as well as female-female and intersexual allopreening. Similarly, female group exploration predicted patterns of sexual harassment, female-female aggression, and female-female as well as male-male allopreening, whilst female group boldness explained patterns of female-female and male-male aggression, as well as male-male and intersexual allopreening. We found no

evidence that group personality composition affected the structure of social hierarchies in either sex. Collectively, these findings suggest the personality of group members can play an important role in the emergence of group-level social patterns and structure. Importantly, we show that the personality composition of one sex can shape social patterns in the opposite sex. Future work is required to explore the underpinning behavioural mechanisms and the fitness consequences of these effects.

Introduction

Sociality is widespread in nature, and social living is thought to be associated with a myriad of fitness benefits (e.g. predator protection and access to social information; Alexander 1974; Altmann 1974; Wrangham 1979; Isbell 1994; Sterck et al. 1997; Rodman 1988), as well as costs (e.g. competition over resources and disease/parasite transmission; Van Schaik et al. 1983; Janson 1988; Daviews et al. 1991; Côté & Poulinb 1995; Borries et al. 2008). The relative costs and benefits of social living may vary, depending on the phenotypic makeup of a group. The individual phenotypic makeup of a group, such as phenotypic averages, variance, or the presence or absence of a particular phenotype, may be referred to as 'group phenotypic composition' (Pruitt & Ferrari 2011; Pruitt & Riechert 2011). Group phenotypic composition may result in emergent group properties that have associated fitness consequences (Wolf & Krause 2014; Farine et al. 2015). For example, the composition of informed versus uninformed individuals in a group may influence emergent group-level behaviours such as collective movement or collective decision making (Farine et al. 2015). Informed individuals may notify groups of resources while uninformed individuals may encourage a majority rules form of consensus; thus, having a mixture of informed and uniformed individuals may result in higher quality group-level decision making, leading to increased fitness (Conradt & Roper 2005; Couzin et al. 2005; 2011; Farine et al. 2015).

Group personality composition is one form of group phenotypic composition that has been shown to be important in determining emergent group properties (Sih & Watters 2005; Pruitt & Ferrari 2011; Pruitt & Riechert 2011). Personality may be defined as between-individual differences in

behaviours, such as aggression, exploration, or boldness, that remain consistent over time and/or across contexts (Dall et al. 2004; Sih et al. 2004; Bell et al. 2009). Personality is often heritable and may be closely linked to fitness gains and losses within an individual (reviewed in Dingemanse and Réale 2005). There may be a feedback loop between personality and social processes, with social processes giving rise to personality, and personality feeding back to affect sociality. On one hand, past work has suggested that interindividual differences in behaviour may arise as a consequence of social processes like social niche specialization (i.e. a decline in social conflict may arise from selection favoring character displacement or diversification Wolf et al. 2007; Bergmüller & Taborsky 2010; Dingemanse & Wolf 2010; Wolf & Weissing 2010). On the other hand, the resulting personality traits may feed back to affect social processes (Wolf & Krause 2014).

In social organisms, patterns of interactions are often nonrandom, with some combinations of individuals interacting more than expected by chance (Dugatkin & Sih 1995; Krause et al. 2007). These nonrandom patterns may be driven by an individual's own phenotype as well as the phenotypes of others in its social environment. One way that personality may affect group-level social processes is by influencing social patterns or structure (Pike et al. 2008; Wolf & Krause 2014). For example, the personality composition of a group has been shown to influence social patterns in water striders (*Aquarius remigis*), affecting the number of successful matings in a group, and ultimately causing differential reproductive success at the group level (Sih & Watters 2005). The effects of group personality composition may also be reflected in the structure of the network of social interactions. Social network analysis provides an informative way to study social structure by examining networks of social links (i.e. edges) between individuals (i.e. nodes; Wey et al. 2008; Krause et al. 2009; Pinter-Wollman et al. 2013). Past work has suggested that personality may affect the social network position of an individual (Pike et al. 2008; Croft et al. 2009; Godfrey et al. 2012; Tanner & Jackson 2012; Aplin et al. 2013). For example, in a wild population of great tits (*Parus major*), slower-exploring individuals may have fewer but stronger connections than faster-exploring individuals (Aplin et al. 2013). Importantly, interindividual differences in network position, that are tied to personality, may

feed back so that group personality composition affects the emergent network structure of a group. However, to the best of our knowledge, no existing studies have examined this possibility.

Understanding the way in which personality affects social relationships is important from an ecology and evolutionary standpoint, as both an individual's network position and the structure of the network at large have been shown to impact an individual's fitness (Silk et al. 2010; Barocas et al. 2011; Formica et al. 2012; Archie et al. 2014; Nuñez et al. 2014; Lehmann et al. 2015; Thompson & Cords 2018). For example, individuals with a greater number of, or stronger, social bonds may have increased survival in adult female chacma baboons (*Papio ursinus*), hamadryas baboons (*P. h. cynocephalus*), and juvenile feral horses (*Equus caballus*; Silk et al. 2010; Archie et al. 2014; Nuñez et al. 2014). Furthermore, it is possible that social network structure may have group-level fitness implications. For example, in great tits, small and medium families with broods having more connected social networks have higher fitness than those with less connected networks, while large families have higher fitness when network connectivity is lower (Royle et al. 2012). Thus, determining whether group personality composition affects the emergent social network structure of a group is an important step toward understanding the ecology and evolution of sociality. Here, we present an investigation into the influence of group personality composition on the emergence of group-level social patterns and social network structure in mixed-sex flocks of red junglefowl (*Gallus gallus*).

In nature, red junglefowl live in small groups with sex-specific social hierarchies that are strongly structured and affect access to mates and other resources (Lill 1966; Thornhill, 1988; Collias et al. 1994; Collias & Collias; 1996; Kim & Zuk, 2000; Pizzari & McDonald 2019). In addition to intrasexual aggression, male red junglefowl aggressively harass females as a form of sexual coercion, and both intra- and intersexual allopreening have been recorded in red junglefowl and in various breeds of the closely related domestic fowl (*Gallus domesticus*; Lill 1968; Vestergaard et al.1993; Leonard et al. 1995; Zimmerman et al. 2006; Kjaer & Bessei 2013). Furthermore, both red junglefowl and domestic fowl exhibit personality related to exploration and boldness, uncorrelated to each other, which may influence the outcomes of social interactions (Favati et al. 2014a; 2014b; 2016; 2017;

2018; Zidar et al. 2017; 2018; Roth et al. in Prep). We have previously shown that in flocks of red junglefowl, these personality traits may also play an important role in intrasexual competition and intersexual interactions. For example, the exploration score of a male and the exploration score of his male competitors can influence aspects of his reproductive performance, such as mating success and the intensity of sperm competition in female-biased groups (Roth et al. in Prep). Similarly, bolder individuals are more likely to mate with shyer partners than expected by chance (Roth et al. in Prep). Given these findings, we expect group personality composition to influence group-level patterns of social dynamics. An individual's behavior may be affected by the phenotypes of actual or potential mates in addition to its own phenotype or the phenotypes of competitors (e.g. Mutzel et al. 2013; David et al. 2015; Santostefano et al. 2016; Roth et al. in Press). Similarly, group-level dynamics related to intrasexual interactions in one sex could be influenced by the group personality compositions of the opposite sex.

In the current study, we therefore examined personality, measured as exploration and boldness at the group level, and explored the influence of male and female group personality composition on emergent group properties related to intersexual harassment, intrasexual aggression, and intra-, and intersexual allopreening. In birds, allopreening, which is analogous to mammal allogrooming, may be viewed as an affiliative interaction and serve both hygienic (de Brooke 1985; Kober & Gaston 2003; Radford & Du Plessis 2006) and social functions (Gaston 1977; Radford & Du Plessis 2006; Emery et al. 2007; Gill 2012; Kenny et al. 2017). Furthermore, allopreening has been shown to positively impact fitness (Lewis et al. 2007). In some cases, allopreening may serve as a mechanism to reduce stress or aggression, resulting in a negative correlation between rates of allopreening and aggression (Harrison 1965; Birkhead 1978; Kober & Gaston 2003; Lewis et al. 2007). However, it is important to note that affiliation and aggression can, in some cases, reflect similar aspects of social relationships (Lehmann et al. 2015). For example, Barbary macaques (*Macaca sylvanus*) may use aggression to compel allogrooming from subordinates (McFarland & Majolo 2011). Similarly, affiliative relationships may be regulated by aggressive interactions in chacma baboons, thus having a stabilizing

effect on social network structure (Barrett et al. 2012). We used four measures of group personality composition: 1) male exploration composition, 2) female exploration composition, 3) male boldness composition, and 4) female boldness composition, and addressed the following three aims.

First, we investigated the role of male and female group personality composition in predicting the frequency of male sexual harassment of females, male-male aggressions, and female-female aggressions, as well as male-male, female-female, and intersexual allopreening. Our work on this population has suggested that bolder males may display a higher ratio of sexual harassment to waltzes (a form of courtship display) toward females (Roth et al. in Prep), and given this, we predicted that groups with higher mean male boldness would result in higher mean harassment of females. Although results are mixed with respect to the directionality of relationships between aggression and personality measures, related to exploration and/or boldness, across species (e.g. Verbeek et al. 1996; Budaev et al. 1999; Guenther et al. 2014; Favati et al. 2017), our work on this population has suggested some evidence that slower exploring females and shyer individuals of both sexes attain higher social status (Roth et al. in Prep). Individuals of certain personality types may be more likely to achieve higher social status due to correlations between personality and aggression (Verbeek et al. 1996; but see Verbeek et al., 1999), and given our previous findings regarding correlations between personality and social status in this population, we predicted that there would be higher mean levels of female-female aggression with slower mean female exploration and lower mean female boldness. We also predicted that there would be higher mean levels of male-male aggression with lower mean male boldness. Our predictions for harassment and aggression informed our set of predictions related to allopreening. We predicted that female-female allopreening would be higher with slower mean female exploration and lower mean female boldness, if allopreening and aggression were part of the same axis. In contrast, we predicted that if affiliation was inversely related to aggression, female-female allopreening would be higher with faster mean female exploration and higher mean female boldness. Furthermore, we predicted that there would be higher mean levels of female-female allopreening with higher mean male boldness, if mean male boldness predicted harassment levels and if female-female social bonds

work to reduce harassment. Similarly, we predicted that intersexual allopreening may be higher with lower mean male boldness, as mean harassment levels may be lower, causing females to be more likely to allopreen with males.

Second, we explored the role of male and female group personality composition in predicting social network structure. Specifically, we explored the effects of group personality composition, as defined above, on: a) the network density of intrasexual aggression, sexual harassment, and intra- as well as intersexual allopreening, b) reciprocity in allopreening networks, and c) global transitivity in intrasexual networks. Network density reflects the realized number of connections in the network out of the total number of potential connections (Wey et al. 2008). Reciprocity is a measure of the proportion of network edges that are bidirectional (i.e. reciprocal), while global transitivity (i.e. clustering coefficient) measures how trios of individuals are related and can be visualized as the proportion of closed triads in the network (i.e. three individuals that are directly connected; Wey et al. 2008). Because exploration relates to how quickly an individual explores an environment, we predicted there would be higher network density in groups with faster mean male and/or female exploration, across interaction types. All else being equal, faster explorers should have a higher encounter rate, as faster moving particles should collide more frequently by chance, giving faster explorers heightened opportunity to interact with more individuals. Furthermore, faster exploring individuals may be more prone to explore their social environment at a higher rate, causing them to interact with more individuals as a direct result of their personality type (but see Firth et al. 2018).

Third, we assessed the role of male and female group personality composition in predicting the linearity and steepness of male and female social hierarchies. The linearity of social hierarchies reflects the number and degree of transitivity of dyadic dominance relationships in a group of competing individuals, while steepness reflects the amount in which individuals differ from one another in winning dominance interactions (Landau 1951; Kendall 1962; Appleby 1983; de Vries 1995; de Vries et al. 2006). The analyses related to social hierarchies were exploratory in nature, and we therefore had no directional predictions.

Methods

Study System

We studied a captive population of red junglefowl housed in outdoor aviaries at the John Krebs Field Station in Wytham, UK. Birds are habituated to humans, and they are provided with *ad libitum* access to food and water, and with individually numbered green Darvic rings, to aid in identification.

Group Personality Composition

Following the methods described in Roth et al. (in Prep), we conducted 30 minute novel arena assays as well as novel object assays, made up of two trials lasting up to 20 minutes each, from 2016 - 2017 to ascertain interindividual variation in exploration and boldness, respectively. We calculated personality scores separately for males and females, as it is likely that the observed behavioral traits serve different functions in the highly sexually dimorphic red junglefowl. Exploration scores ranged from -2.173 to 3.792 (mean = 0.293 ± 1.530) in males and -1.746 to 4.145 (mean = 0.932 ± 1.567) in females, and boldness scores ranged from -2.322 to 1.937 (mean = -0.019 ± 1.232) in males and -3.899 to 1.584 (mean = -0.002 ± 1.429) in females. Measures for both behavioral traits showed moderate to high repeatability, although repeatability for male boldness was not significant (Male exploration: repeatability = 0.538, 95% CI = 0.351 - 0.591; Female exploration: repeatability = 0.479, 95% CI = 0.260 - 0.554; Male boldness: repeatability = 0.226, 95% CI = -0.027 - 0.246; and Female boldness: repeatability = 0.355, 95% CI = 0.050 - 0.470). Exploration and boldness were not correlated in either sex (males: $r = 0.170$; $p = 0.209$, N=56; females: $r = 0.064$, $p = 0.704$, $N = 38$).

We defined group personality composition as the mean exploration score and mean boldness score in each group, calculated separately for male and female group members. However, the mean is highly dependent on the distribution of personality scores (e.g. a group of individuals with intermediate personality types could show the same mean as a group of individuals consisting of an even split of extreme phenotypes). Given this, we conducted a parallel set of analyses where group

personality composition was defined as the proportion of fast or bold explorers in a group. For these analyses, individuals with a behavioral score >0 were considered fast or bold, and individuals with a score <0 were considered slow or shy. Tables containing the model outputs for these auxillary analyses can be found in the supplementary information. Measuring group personality composition as the proportion of individuals with a certain phenotype has its own limitations, notably that information is lost when continuously distributed variables are binned into arbitrary binary categories. For this reason, we felt it was prudent to use a dual approach. Thus, when interpreting our results, we only discuss those effects that were supported as significant or close to significant ($p < 0.10$) by both sets of models.

Social groups

We generated 24 mixed-sex groups, manipulating the ratios of fast- to slow-exploring males and fast- to slow-exploring females (Roth et al. in Prep; range of mean male exploration = -0.274 - 1.323; range of mean female exploration = -0.265 - 1.655). Groups also differed in the ratio of bold to shy males and bold to shy females (range of mean male boldness = -1.150 - 1.348; range of mean female boldness = -0.666 - 0.837). Each group contained 12 individuals and were composed of one of three different sex ratios: male biased (9 males and 3 females; 8 groups), even-sex ratio (6 males and 6 females; 8 groups), and female-biased (3 males and 9 females; 8 groups). Past work on natural or seminatural populations have reported groups ranging in size from 2 – 20 individuals with highly variable sex ratios spanning anywhere from all male groups to mostly female groups (e.g. ca. 78% female; Collias & Collias 1967; 1996; Javed & Rahmani 2000). For each sex ratio, we observed half of the groups during the breeding season from May to August 2016 and half from April to July 2017. Each group was housed in a 11.5 × 7.2 m pen, and we gave males ca. 24 hours to establish a social hierarchy prior to the introduction of females at 1:00 PM on the day of the first evening observation. We performed observations recording ad libitum data on intrasexual aggressive interactions (chases, lunges, aggressive pecking, and fights), avoidances, allopreening, and intersexual harassment for 6

evenings (three hours before sunset to sunset, local time) and 5 mornings (sunrise to three hours after sunrise, local time), for a total of 11 sampling periods. We recorded the actor and receiver of all interactions, besides fights, where both involved individuals were considered actors, as aggression during such encounters is bidirectional. We defined allopreening as gentle nuzzling of a conspecific's body, in which soft nibbling of the feathers or underlying skin was observed, rather than pecking, and also as light pecking of a conspecific's beak or face to remove food particles (Lill 1968; Leonard et al. 1995; Zimmerman et al. 2006). Although some studies on fowl combine allopreening and feather pecking (i.e. pecking at or pulling out feathers; e.g. Nätt et al. 2007; Castellini et al. 2016), these behaviors are generally viewed as separate in fowl (Vestergaard et al.1993; Leonard et al. 1995; Zimmerman et al. 2006; Kjaer & Bessei 2013), and we did not did not include any feather pecking we observed as allopreening.

Emergent group social properties

We examined six group-level social properties: 1) mean number of interactions, 2) network density, 3) network transitivity, 4) reciprocity, 5) linearity of social hierarchies, and 6) steepness of social hierarchies. For mean number of interactions, we calculated the mean number of interactions recorded within each of the 11 sampling periods, rather than across all sampling periods. We calculated the mean number of male sexual harassment of females, male-male and female-female aggression, as well as male-male, female-female and intersexual allopreening (either female to male or male to female), for each sampling period, for each of the 24 groups. For all interaction types, except for harassments, we divided the total number of a given interaction type in each of the 11 sampling periods by the number of potential actors, to obtain a mean interaction number for each sampling period. For example, if 30 female-female aggressions were observed during the course of a sampling period in a group with 6 females, we computed a mean of 5 aggressions/individual for this period. For harassments, we focused on the receiver, dividing the total number of harassments in each of the 11 sampling periods by the number of potential female recipients.

In social networks, social links, or edges, may be defined by behavioural interactions or by spatial or temporal proximity (Wey et al. 2008; Krause et al. 2009; Pinter-Wollman et al. 2013). They may be directed, in cases where behavioural interactions have an actor and receiver, or undirected, when there is no obvious directionality to an encounter. Furthermore, network edges may be weighted to reflect the relative number of observed encounters between individuals. Unweighted edges simply imply that two individuals are connected but give no indication of the strength of such relationships (Wey et al. 2008; Krause et al. 2009; Pinter-Wollman et al. 2013). We calculated network density across all sampling periods, dividing the number of unweighted realized network edges (i.e. interacting dyads) by the number of unweighted potential edges. We used directed networks, where edges were formed from actors to receivers. We composed aggression networks using lunges, chases, aggressive pecks, and fights. For fights, we created edges in both directions, given mutual aggression. We calculated reciprocity and global transitivity using the 'igraph' package (Csardi & Nepusz 2006) in R 3.3.2 (R Core Team, 2018).

We assessed social status, considering all intrasexual aggressive interactions (chases, lunges, aggressive pecking, and fights) and avoidances. Using R, we calculated the linearity of social hierarchies using in the 'compete' package (Curley 2019) and calculated the steepness of social hierarchies using the 'steepness' package (de Vries et al. 2006; Leiva & de Vries 2014).

Statistical methods

We used R 3.3.2 for all analyses (R Core Team, 2018). To assess the relationship between group personality composition and mean number of interactions, we ran separate generalized linear mixed models (GLMM) for harassment, male-male aggression, female-female aggression, male-male allopreening, female-female allopreening, and intersexual allopreening. We included male exploration composition, female exploration composition, male boldness composition, and female boldness composition, in addition to sex ratio, as fixed effects. We included group identity and period number (i.e. 1-11) as random effects. We also included female group identity as a random effect because we

reused four female group compositions two times each. We reused female groups because the number of available females was limited (see McDonald et al. 2017; Roth et al. in Prep for a similar approach). When results suggested a significant effect of one or more categories for group sex ratio, compared to the intercept, we conducted a likelihood ratio test, comparing models with and without sex ratio, to examine the overall effect of sex ratio. Harassment and male-male aggression occurred regularly, and we used a GLMM with a gamma family and log link for analyses related to harassment and male-male aggression. In contrast, datasets for female-female aggression, female-female allopreening, and intersexual allopreening were heavily zero inflated, and we therefore used a two-step approach for analyses based on these interaction types. We first used a GLMM with a binomial family to test whether group personality compositions could predict the probability of the occurrence of these behavioral interactions. We then used a GLMM with a gamma family and log link to examine whether group personality compositions could predict the mean number of interactions, when at least one interaction was observed. Because male-male allopreening occurred very rarely, there was not enough variation to run a second model examining how group phenotypic composition influenced the level of male-male allopreening, and we only ran a model that examined whether group personality compositions predicted the probability of male-male allopreening.

To assess the relationship between group personality composition and network density, we ran separate generalized linear models with a binomial family for networks created from the six different measures (i.e. harassments, male-male aggression, female-female aggression, male-male allopreening, female-female allopreening, and intersexual allopreening). The response variable consisted of the proportion of potential edges that were observed. We included sex ratio, male group exploration composition, female group exploration composition, male group boldness composition, and female group boldness composition as fixed effects. To examine the relationship between group personality composition and reciprocity in allopreening networks, we ran linear models with reciprocity as the response and male group exploration composition, female group exploration composition, male group boldness composition, female group boldness composition, and sex ratio as fixed effects. Given that

male-male allopreening only occurred in 13 out of 24 groups, we only examined predictors of reciprocity in female-female and heterosexual allopreening networks. To evaluate the relationship between group personality composition and transitivity intrasexual networks, we ran linear models with transitivity as the response and male group exploration composition, female group exploration composition, male group boldness composition, female group boldness composition, and sex ratio as fixed effects. Distributions for all transitivity response variables could not be transformed to normality, and given this, results should be taken with caution. Because transitivity across female-female allopreening networks was just shy of normality (Shapiro-Wilk normality test: $W = 0.914$; $p = 0.049$), we ran a linear model on the raw data. We conducted arcsine transformations on transitivity values arising from male-male and female-female aggression networks to bring distributions closer to normality and ran linear models on the arcsine transformed data. We did not examine transitivity for male-male allopreening networks, given that male-male allopreening was only observed in 13 out of 24 replicate groups. Moreover, we did not examine transitivity in heterosexual networks, because individuals could only interact with the opposite sex, meaning that closed triads could never be formed (i.e. 3 individuals could never have three edges between them because males could not interact with males and females could not interact with females). For all social network analyses, we did not need to use any of the randomization methods commonly employed to control for nonindependence in social networks, because we observed network-level metrics in 24 replicate groups (Bhadra et al. 2009; Darden et al. 2009; Croft et al. 2011).

To assess the relationship between group personality composition and the steepness of male and female social hierarchies, we ran linear models with steepness as the response and male group exploration composition, female group exploration composition, male group boldness composition, female group boldness composition, and sex ratio as fixed effects. Linearity was only significant in eight of 24 groups for male social hierarchies. Similarly, we did not have enough information to create social hierarchies for two female groups, but of the 22 groups where linearity could be calculated, linearity was only significant for nine groups. Given this, we assessed whether group personality

composition could predict whether the linearity of social hierarchies was significant. We ran generalized linear models with a binomial family and a response of whether or not linearity was significant (0 = not significant; 1 = significant). We included male group exploration composition, female group exploration composition, male group boldness composition, female group boldness composition, and sex ratio as fixed effects.

Results

Descriptive statistics (means, standard deviations, and ranges) of the mean number, network density, network transitivity, and reciprocity of harassments, male-male aggressions, female-female aggressions, male-male allopreening, female-female allopreening, and/or intersexual allopreening and of the steepness of sex-specific social hierarchies are presented in Table S1. Graphs of the different social networks are presented in Figures S1 – S6.

i) Group personality composition and the frequency of behavioural interactions.

The mean number of harassments was lower when mean female exploration was faster (Table 1; Figure 1). This relationship remained when we defined group personality composition as the proportion of fast exploring females in a group (Tables S2). The mean number of harassments observed was not predicted by male group exploration composition, male group boldness composition, or female group boldness composition (Tables 1 & S2). As expected, females in female-biased groups were, on average, exposed to a lower rate of harassment, and females in male-biased groups to a higher rate of harassment, compared to even sex ratio groups, when group personality composition was defined as mean personality scores and when it was defined as the proportion individuals of a certain personality type (Tables 1 & S2). Likelihood ratio tests comparing models with and without the fixed effect of sex ratio revealed a significant overall effect of sex ratio (Mean group personality: Chi-squared = 21.633, df =2, $p < 0.001$; Proportion of personality types: Chi-squared = 20.940, df =2, $p < 0.001$).

Table 1. The effects of mean male exploration, mean male boldness, mean female exploration, mean female boldness, and sex ratio on the mean number of harassments, mean number of male-male aggressive interactions, whether female-female aggression occurred, and the mean number of female-female aggressive interactions that occurred when female-female aggression was observed. (See text for details.)

Predictor	Est. ± SE	z-value	p
Harassment: Mean			
Mean Exploration Males	0.042 ± 0.151	0.276	0.783
Mean Boldness Males	-0.004 ± 0.124	-0.032	0.975
Mean Exploration Females	-0.367 ± 0.130	-2.809	**0.005**
Mean Boldness Females	0.217 ± 0.174	1.249	0.212
Sex Ratio: Male Biased	0.749 ± 0.166	4.517	**<0.001**
Sex Ratio: Female Biased	-0.714 ± 0.192	-3.728	**<0.001**
Male-Male Aggression: Mean			
Mean Exploration Males	-4.459e-02 ± 1.589e-01	-0.281	0.779
Mean Boldness Males	1.131e-01 ± 1.352e-01	0.836	0.403
Mean Exploration Females	8.183e-02 ± 1.322e-01	0.619	0.536
Mean Boldness Females	-2.619e-05 ± 1.656e-01	0	1.000
Sex Ratio: Male Biased	-1.457e-01 ± 1.615e-01	-0.902	0.367
Sex Ratio: Female Biased	3.397e-01 ± 1.819e-01	1.868	0.062^{+}
Female-Female Aggression: Binary			
Mean Exploration Males	-3.156 ± 1.077	-2.931	**0.003**$^{++}$
Mean Boldness Males	1.628 ± 0.763	2.135	**0.033**$^{++}$
Mean Exploration Females	2.314 ± 0.635	3.644	**<0.001**
Mean Boldness Females	-2.653 ± 1.032	-2.572	**0.010**
Sex Ratio: Male Biased	-4.158 ± 0.873	-4.762	**<0.001**
Sex Ratio: Female Biased	-1.166 ± 1.498	-0.778	0.436
Female-Female Aggression: Mean			
Mean Exploration Males	-0.379 ± 0.196	-1.933	0.053
Mean Boldness Males	0.115 ± 0.154	0.741	0.458
Mean Exploration Females	0.078 ± 0.187	0.415	0.678
Mean Boldness Females	-0.200 ± 0.247	-0.809	0.418
Sex Ratio: Male Biased	-0.008 ± 0.245	-0.032	0.974
Sex Ratio: Female Biased	0.628 ± 0.262	2.394	**0.017**

"+" denotes that when group personality composition was defined as 1) mean personality or 2) the proportion of individuals with a certain personality type, the relationship was significant under one definition and marginally non-significant ($p < 0.10$) under the other definition. In contrast, "++" denotes that the relationship was significant under one definition and not significant under the other.

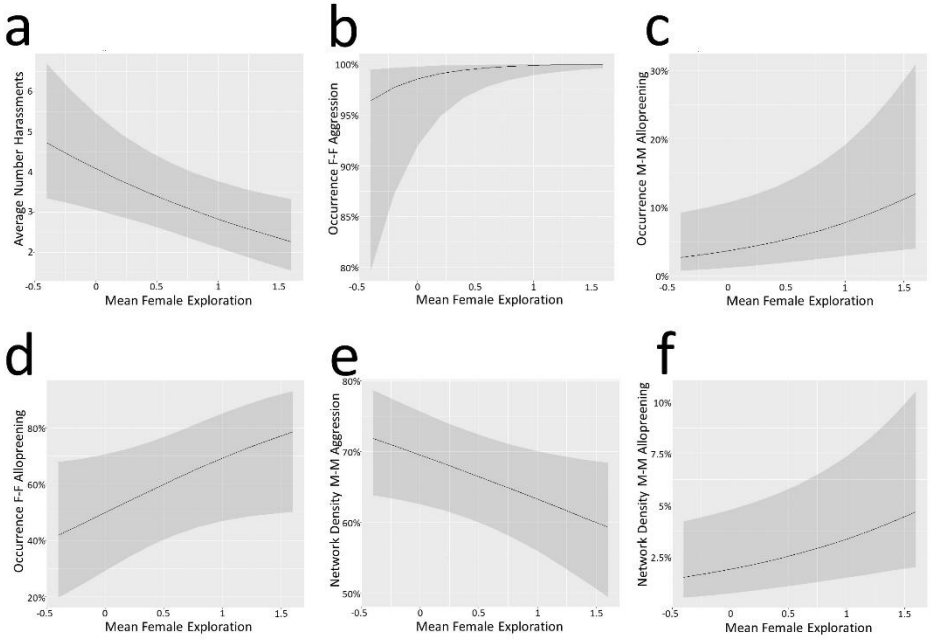

Figure 1. The effects of mean female exploration on: a) the average number of harassments in a group, b) the occurrence of female-female ("F-F") aggression in a group, c) the occurrence of male-male ("M-M") allopreening in a group, d) the occurrence of female-female ("F-F") allopreening in a group, e) male-male ("M-M") aggression network density, and f) male-male ("M-M") allopreening network density.

None of the measures of group personality composition predicted the mean number of male-male aggressive interactions when group personality composition was defined as either the mean personality score or the proportion of individuals of a given personality type. We found that when group personality composition was defined as the proportion of individuals with a certain personality type, the mean number of male-male aggressions was higher in female-biased groups than in even sex ratio groups; and when group personality composition was calculated as the mean personality score of a group, this relationship was marginally non-significant (Mean group personality: Chi-squared = 3.465, df =2, p = 0.176; Proportion of personality types: Chi-squared = 4.399, df =2, p = 0.111; Tables 1 & S2).

Female-female aggression was more likely to occur in groups with faster mean female exploration and in groups with lower mean female boldness (Table 1; Figures 1 & 2). This was also the case when group personality composition was defined as the proportion of a given personality type (Table S2). Similarly, female-female aggression was more likely to occur in groups with slower mean male exploration and in groups with higher mean male boldness, however this was only the case when group personality composition was defined as the mean personality score, but not when it was defined as the proportion of a given personality type (Tables 1 & S2). When group personality composition was defined both as mean personality scores and as the proportion of individuals with a certain personality type, female-female aggression was less likely to be seen in male-biased groups, compared to even sex ratio groups (Mean group personality: Chi-squared = 23.149, df =2, $p < 0.001$; Proportion of personality types: Chi-squared = 17.815, df =2, $p < 0.001$; Tables 1 & S2). When analyzing variation in the mean number of female-female aggressive interactions in the subset of data where female aggression occurred, group personality composition in any of the tested forms had no effect on the mean number of female-female aggressive interactions observed (Tables 1 & S2). Female-biased groups had a higher mean number of aggressive female-female interactions, compared to even sex ratio groups, when group personality composition was defined using mean personality scores and when it was defined as the proportion of individuals with a certain personality type (Mean group personality: Chi-squared = 5.866, df =2, $p = 0.053$; Proportion of personality types: Chi-squared = 7.132, df =2, $p = 0.028$; Tables 1 & S2).

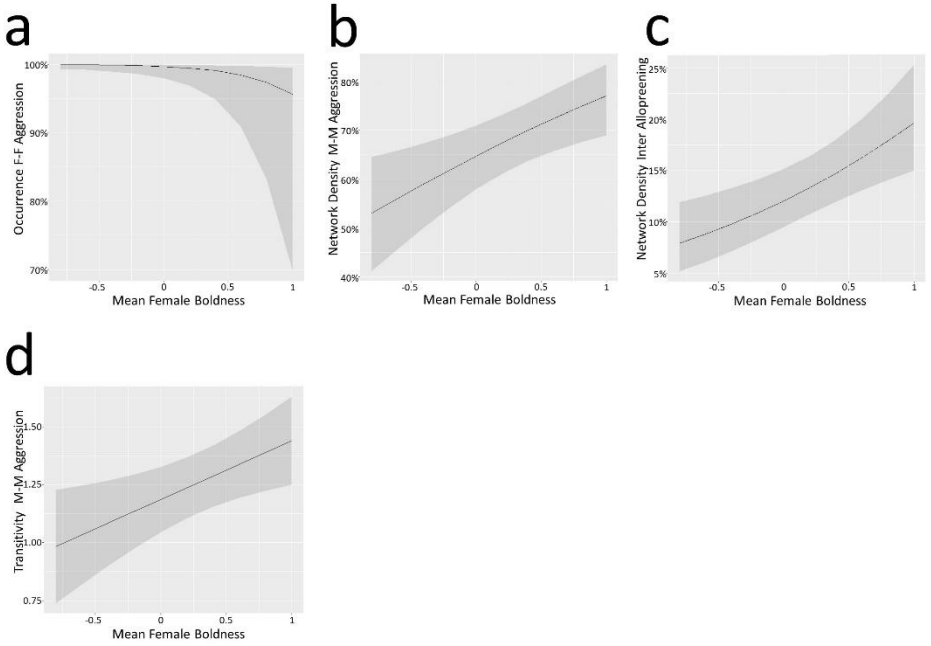

Figure 2. The effects of mean female boldness on: a) the occurrence of female-female ("F-F") aggression in a group, b) male-male ("M-M") aggression network density, c) intersexual ("Inter") allopreening network density, and d) male-male ("M-M") aggression network transitivity with arcsin transformation.

Male-male allopreening was more likely to occur when mean female exploration was faster and when the proportion of fast exploring females was higher, but female boldness composition, male boldness composition, and male exploration composition had no effect of the likelihood of male-male allopreening, regardless of whether group personality composition was defined as a mean or a proportion (Tables 2 & S3; Figure 1). Male-male allopreening was more likely to occur in male-biased groups, compared to even sex ratio groups, both when group personality composition was defined as mean personality scores and when it was defined as defined as the proportion individuals of a certain personality type (Mean group personality: Chi-squared = 32.398, df =2, $p << 0.001$; Proportion of personality types: Chi-squared = 38.478, df =2, $p << 0.001$; Tables 2 & S3).

Table 2. The effects of mean male exploration, mean male boldness, mean female exploration, mean female boldness, and sex ratio on the occurrence of male-male allopreening, the occurrence of female-female allopreening, the mean number of female-female allopreening interactions that occurred when female-female allopreening was observed, the occurrence of intersexual allopreening, and the mean number of intersexual allopreening interactions that occurred when female-female allopreening was observed. (See text for details.)

Predictor	Est. ± SE	z-value	p
Male-Male Allopreening: Binary			
Mean Exploration Males	0.107 ± 0.555	0.193	0.847
Mean Boldness Males	-0.644 ± 0.512	-1.258	0.208
Mean Exploration Females	0.802 ± 0.368	2.180	**0.029**
Mean Boldness Females	-0.603 ± 0.588	-1.025	0.305
Sex Ratio: Male Biased	2.883 ± 0.549	5.248	**<0.001**
Sex Ratio: Female Biased	-1.761 ± 1.168	-1.508	0.132
Female-Female Allopreening: Binary			
Mean Exploration Males	0.991 ± 0.524	1.892	0.058^{+}
Mean Boldness Males	-0.541 ± 0.466	-1.160	0.246^{++}
Mean Exploration Females	0.814 ± 0.446	1.824	0.068^{+}
Mean Boldness Females	-0.085 ± 0.594	-0.143	0.886
Sex Ratio: Male Biased	-0.723 ± 0.544	-1.328	0.184
Sex Ratio: Female Biased	2.081 ± 0.674	3.086	**0.002**
Female-Female Allopreening: Mean			
Mean Exploration Males	0.087 ± 0.180	0.485	0.628
Mean Boldness Males	-0.207 ± 0.152	-1.360	0.174
Mean Exploration Females	0.079 ± 0.158	0.503	0.615
Mean Boldness Females	0.090 ± 0.194	0.462	0.644
Sex Ratio: Male Biased	0.127 ± 0.205	0.620	0.535
Sex Ratio: Female Biased	-0.154 ± 0.212	-0.728	0.467
Intersexual Allopreening: Binary			
Mean Exploration Males	0.597 ± 0.624	0.956	0.339
Mean Boldness Males	-0.602 ± 0.532	-1.132	0.258
Mean Exploration Females	0.195 ± 0.540	0.361	0.718
Mean Boldness Females	0.726 ± 0.668	1.086	0.278
Sex Ratio: Male Biased	1.807 ± 0.672	2.689	**0.007**
Sex Ratio: Female Biased	1.268 ± 0.714	1.776	0.076
Intersexual Allopreening: Mean			
Mean Exploration Males	0.077 ± 0.293	0.262	0.793
Mean Boldness Males	-0.283 ± 0.249	-1.138	0.255
Mean Exploration Females	-0.098 ± 0.236	-0.416	0.677
Mean Boldness Females	0.276 ± 0.298	0.926	0.355
Sex Ratio: Male Biased	0.702 ± 0.295	2.383	**0.017**
Sex Ratio: Female Biased	0.436 ± 0.337	1.292	0.197

"+" denotes that when group personality composition was defined as 1) mean personality or 2) the proportion of individuals with a certain personality type, the relationship was significant under one definition and marginally non-significant ($p < 0.10$) under the other definition. In contrast, "++" denotes that the relationship was significant under one definition and not significant under the other.

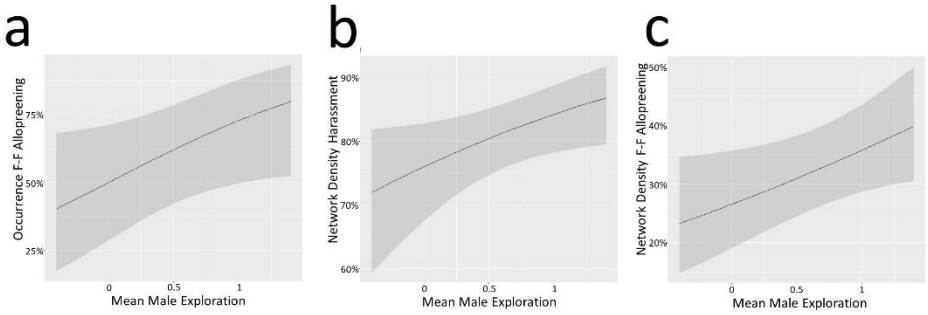

Figure 3. The effects of mean male exploration on: a) the occurrence of female-female ("F-F") allopreening in a group, b) harassment network density, and c) female-female ("F-F") allopreening network density.

Female-female allopreening was more likely to occur when there was a higher proportion of fast exploring females, a higher proportion of fast exploring males, and a lower proportion of bold males in a group (Table S3). However, when group personality composition was defined as mean personality, the effects of mean male and female exploration were marginally non-significant, while mean male boldness did not have an effect (Table 2; Figures 1 & 3). Female-female allopreening was also more likely to occur in female-biased groups than in even sex ratio groups, when group personality composition was calculated using mean personality scores and when it was calculated as the proportion individuals of a certain personality type (Mean group personality: Chi-squared = 16.175, df =2, $p << 0.001$; Proportion of personality types: Chi-squared = 23.100, df =2, $p << 0.001$; Tables 2 & S3). There were no significant predictors of the mean number of female-female allopreening interactions observed among the subset of data where female-female allopreening was seen, regardless of how group personality composition was defined (Tables 2 & S3).

We found no effect of male or female exploration or boldness composition on either the occurrence of intersexual allopreening, or the mean number of intersexual allopreening interactions, in the subset where intersexual allopreening occurred. This was the case both when group personality

composition was defined as mean group personality, as well as when it was defined as the proportion of individuals with a certain personality type (Tables 2 & S3). For both definitions, however, we found that the occurrence and mean number of intersexual allopreening interactions were higher in male-biased groups than in even sex ratio groups (Occurrence - Mean group personality: Chi-squared = 8.222, df =2, p = 0.016; Proportion of personality types: Chi-squared = 9.567, df =2, p = 0.008; Mean Number - Mean group personality: Chi-squared = 4.463, df =2, p = 0.008; Proportion of personality types: Chi-squared = 4.555, df =2, p = 0.107; Tables 2 & S3).

ii) Group personality composition and network density, reciprocity, and transitivity.

Harassment networks were denser in groups with a faster mean male exploration (Table 3; Figure 3). Similarly, when group personality composition was defined as the proportion of individuals with a certain personality type, there was a trend for harassment networks to be denser in groups with a higher proportion of fast-exploring males (Table S4). Male- and female-biased groups had denser harassment networks than even sex ratio groups, both when group personality composition was defined using mean personality scores and when it was defined as the proportion of individuals with a certain personality type (Mean group personality: Deviance = -7.401, df = -2, p = 0.025; Proportion of personality types: Deviance = -8.341, df = -2, p = 0.015; Tables 3 & S4).

Table 3. The effects of mean male exploration, mean male boldness, mean female exploration, mean female boldness, and sex ratio on harassment, male-male aggression, and female-female aggression network densities. (See text for details.)

Predictor	Est. ± SE	z-value	p
Harassment			
Mean Exploration Males	0.523 ± 0.247	2.119	**0.034**$^{+}$
Mean Boldness Males	-0.083 ± 0.226	-0.369	0.712
Mean Exploration Females	-0.390 ± 0.226	-1.725	0.085
Mean Boldness Females	0.452 ± 0.280	1.615	0.106
Sex Ratio: Male Biased	0.687 ± 0.286	2.400	**0.016**
Sex Ratio: Female Biased	0.674 ± 0.303	2.220	**0.026**
Male-Male Aggression			
Mean Exploration Males	0.092 ± 0.197	0.464	0.642^{++}
Mean Boldness Males	-0.175 ± 0.179	-0.974	0.330
Mean Exploration Females	-0.280 ± 0.134	-2.086	**0.037**
Mean Boldness Females	0.604 ± 0.197	3.070	**0.002**
Sex Ratio: Male Biased	-0.005 ± 0.171	-0.031	0.976
Sex Ratio: Female Biased	1.001 ± 0.409	2.446	**0.014**
Female-Female Aggression			
Mean Exploration Males	-0.124 ± 0.198	-0.628	0.530
Mean Boldness Males	0.209 ± 0.148	1.413	0.158
Mean Exploration Females	-0.044 ± 0.176	-0.250	0.803
Mean Boldness Females	0.109 ± 0.202	0.540	0.589
Sex Ratio: Male Biased	-0.101 ± 0.323	-0.312	0.755
Sex Ratio: Female Biased	-0.050 ± 0.197	-0.253	0.800

"+" denotes that when group personality composition was defined as 1) mean personality or 2) the proportion of individuals with a certain personality type, the relationship was significant under one definition and marginally non-significant ($p < 0.10$) under the other definition. In contrast, "++" denotes that the relationship was significant under one definition and not significant under the other.

Male-male aggression network density was higher when there was a slower mean female exploration score and when there was a higher mean female boldness score (Table 3; Figures 1 & 2). Similarly, when group personality composition was defined as the proportion of individuals with a certain personality type, networks were denser when there was a lower proportion of fast exploring females and when there was a higher proportion of bold females (Table S4). Furthermore, when group personality composition was defined as the proportion, but not as the mean, there was also a significant effect of male exploration composition, with groups containing a lower proportion of fast exploring males expressing denser male-male aggression networks (Table S4). Male-male aggression networks were denser in female-biased groups than in even sex ratio groups under both definitions of group personality composition (Mean group personality: Deviance = -7.904, df = -2, p = 0.019; Proportion of personality types: Deviance = -5.250, df = -2, p = 0.072; Tables 3 & S4).

Female-female aggression network density was not significantly affected by male or female exploration or boldness composition or by the sex ratio of a group, regardless of whether group personality composition was defined as the mean personality score or as the proportion of individuals with a certain personality type (Tables 3 & S4).

Male-male allopreening networks were denser in groups with a faster mean female exploration and a lower mean female boldness (Table 4; Figure 1). However, while female group exploration composition remained a significant predictor of male-male allopreening network density when group personality composition was defined as the proportion of individuals with a certain personality type, female boldness composition did not (Table S5). Under both definitions of group personality composition, male-male allopreening networks were denser in male-biased, compared to even sex ratio, groups (Mean group personality: Deviance = -17.754, df = -2, $p < 0.001$; Proportion of personality types: Deviance = -14.484, df = -2, $p = 0.001$; Tables 4 & S5).

Table 4. The effects of mean male exploration, mean male boldness, mean female exploration, mean female boldness, and sex ratio on male-male allopreening, female-female allopreening, and intersexual network densities. (See text for details.)

Predictor	Est. ± SE	z-value	p
Male-Male Allopreening			
Mean Exploration Males	0.745 ± 0.503	1.480	0.139
Mean Boldness Males	-0.271 ± 0.373	-0.727	0.467
Mean Exploration Females	0.580 ± 0.234	2.478	**0.013**
Mean Boldness Females	-1.079 ± 0.463	-2.332	**0.020**$^{++}$
Sex Ratio: Male Biased	1.391 ± 0.447	3.113	**0.002**
Sex Ratio: Female Biased	-0.426 ± 1.111	-0.383	0.702
Female-Female Allopreening			
Mean Exploration Males	0.434 ± 0.209	2.074	**0.038**
Mean Boldness Males	-0.371 ± 0.158	-2.351	**0.019**
Mean Exploration Females	-0.029 ± 0.189	-0.154	0.878
Mean Boldness Females	-0.010 ± 0.214	-0.048	0.962
Sex Ratio: Male Biased	0.637 ± 0.327	1.951	0.051^{+}
Sex Ratio: Female Biased	-0.025 ± 0.212	-0.116	0.908
Intersexual Allopreening			
Mean Exploration Males	0.027 ± 0.163	0.168	0.866
Mean Boldness Males	-0.363 ± 0.138	-2.634	**0.008**$^{+}$
Mean Exploration Females	-0.263 ± 0.129	-2.042	**0.04**1^{++}
Mean Boldness Females	0.580 ± 0.171	3.386	**0.001**
Sex Ratio: Male Biased	1.172 ± 0.165	7.110	**<0.001**
Sex Ratio: Female Biased	0.946 ± 0.194	4.878	**<0.001**

"+" denotes that when group personality composition was defined as 1) mean personality or 2) the proportion of individuals with a certain personality type, the relationship was significant under one definition and marginally non-significant ($p < 0.10$) under the other definition. In contrast, "++" denotes that the relationship was significant under one definition and not significant under the other.

Female-female allopreening networks were denser in groups with faster mean male exploration scores and lower mean male boldness scores (Table 4; Figures 3 & 4). Similarly, female-female allopreening networks were denser in groups with a greater proportion of fast-exploring males and a smaller proportion of bold males (Table S5). When group personality composition was defined as the proportion of individuals with a certain personality type, male-biased groups experienced denser female-female allopreening networks than even sex ratio groups (Deviance = -4.000, df = -2, p = 0.135; Table S5). The difference in network density between male-biased and even sex ratio groups was marginally non-significant when group phenotypic composition was defined as mean personality (Deviance = -4.587, df = -2, p = 0.101; Table S5).

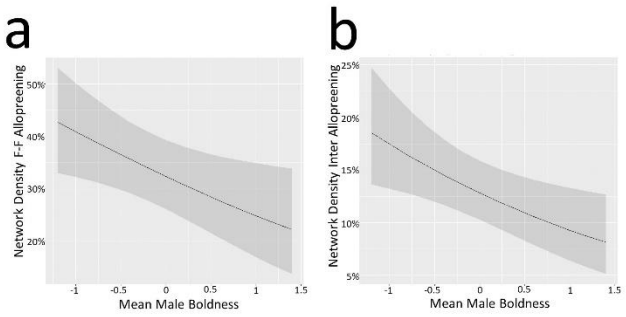

Figure 4. The effects of mean male boldness on: a) female-female ("F-F") allopreening network density and b) intersexual ("Inter") allopreening network density.

Intersexual allopreening networks were denser in groups with lower mean male boldness, higher mean female boldness, and slower mean female exploration (Table 4; Figures 2 & 4). Although the effect of female boldness composition was significant when group personality composition was defined as the proportion of individuals with a certain personality type, the negative relationship between the proportion of bold males and intersexual allopreening network density was barely non-significant, while the effects of the proportion of fast exploring females was not significant (Table S5). Intersexual allopreening network density was higher in male- and female-biased groups compared to even sex ratio groups using either measure of group personality composition (Mean group personality: Deviance = -55.307, df = -2, $p < 0.001$; Proportion of personality types: Deviance = -52.309, df = -2, $p < 0.001$; Tables 4 & S5).

Group personality composition in any form did not predict reciprocity in female-female allopreening networks (Tables 5 & S6). However, reciprocity in female-female allopreening networks was higher in male-biased groups, compared to even sex ratio groups, when group personality composition was defined as the proportion of a given personality type (Sum of squares = -0.181, df = -2, $p = 0.138$; Table S6). This relationship was slightly non-significant when group personality

composition was defined as mean personality score (Sum of squares = -0.255, df = -2, p = 0.056; Table 5).

The reciprocity of intersexual allopreening was higher in groups with a higher proportion of bold females, however, female boldness composition was not a significant predictor of reciprocity when it was defined as mean female boldness (Tables 5 & S6). Reciprocity in intersexual allopreening networks was higher in male-biased groups, compared to even sex ratio groups, when group personality composition was defined as mean personality score and when it was defined as the proportion of a given personality type (Mean group personality: Sum of squares = -0.371, df = -2, p = 0.001; Proportion of personality types: Sum of squares = -0.394, df = -2, p < 0.001; Tables 5 & S6).

Table 5. The effects of mean male exploration, mean male boldness, mean female exploration, mean female boldness, and sex ratio on reciprocity in female-female allopreening and intersexual allopreening networks. (See text for details.)

Predictor	Est. ± SE	t-value	p
Female-Female Allopreening			
Mean Exploration Males	-0.010 ± 0.110	-0.088	0.931
Mean Boldness Males	-0.131 ± 0.093	-1.402	0.180
Mean Exploration Females	0.025 ± 0.095	0.262	0.797
Mean Boldness Females	0.134 ± 0.115	1.163	0.262
Sex Ratio: Male Biased	-0.223 ± 0.116	-1.932	0.071^{+}
Sex Ratio: Female Biased	-0.074 ± 0.125	-0.592	0.562
Intersexual Allopreening			
Mean Exploration Males	-0.062 ± 0.080	-0.777	0.448
Mean Boldness Males	-0.003 ± 0.068	-0.039	0.970
Mean Exploration Females	0.088 ± 0.066	1.323	0.203
Mean Boldness Females	0.130 ± 0.083	1.567	0.136^{++}
Sex Ratio: Male Biased	0.314 ± 0.081	3.882	**0.001**
Sex Ratio: Female Biased	0.163 ± 0.091	1.787	0.092

"+" denotes that when group personality composition was defined as 1) mean personality or 2) the proportion of individuals with a certain personality type, the relationship was significant under one definition and marginally non-significant (p < 0.10) under the other definition. In contrast, "++" denotes that the relationship was significant under one definition and not significant under the other.

Transitivity of male-male aggression networks was higher with higher mean female boldness and with higher proportions of bold females (Tables 6 & S7; Figure 2). When group personality composition was defined as mean personality score and when it was defined as the proportion of a given personality type in a group, transitivity of male-male aggression networks was higher in female-biased groups, compared to even sex ratio groups (Mean group personality: Sum of squares = -0.858, df = -2, $p < 0.001$; Proportion of personality types: Sum of squares = -0.599, df = -2, $p < 0.001$).

Table 6. The effects of mean male exploration, mean male boldness, mean female exploration, mean female boldness, and sex ratio on male-male aggression, female-female aggression, and female-female allopreening network transitivity. (See text for details.)

Predictor	Est. ± SE	t-value	p
Male-Male Aggression			
Mean Exploration Males	0.080 ± 0.094	0.851	0.407
Mean Boldness Males	-0.119 ± 0.080	-1.497	0.153
Mean Exploration Females	0.058 ± 0.078	0.747	0.466
Mean Boldness Females	0.254 ± 0.098	2.600	**0.019**
Sex Ratio: Male Biased	-0.015 ± 0.095	-0.154	0.879
Sex Ratio: Female Biased	0.450 ± 0.107	4.197	**0.001**
Female-Female Aggression			
Mean Exploration Males	-0.065 ± 0.137	-0.474	0.642
Mean Boldness Males	0.026 ± 0.116	0.225	0.825
Mean Exploration Females	0.006 ± 0.117	0.051	0.960
Mean Boldness Females	-0.082 ± 0.142	-0.574	0.574
Sex Ratio: Male Biased	0.412 ± 0.149	2.761	**0.015**
Sex Ratio: Female Biased	-0.123 ± 0.148	-0.826	0.422
Female-Female Allopreening			
Mean Exploration Males	0.234 ± 0.170	1.374	0.188
Mean Boldness Males	0.072 ± 0.144	0.498	0.625
Mean Exploration Females	0.117 ± 0.146	0.802	0.434^{++}
Mean Boldness Females	0.062 ± 0.177	0.348	0.732
Sex Ratio: Male Biased	0.271 ± 0.178	1.523	0.147
Sex Ratio: Female Biased	0.340 ± 0.192	1.769	0.096

"++" denotes that when group personality composition was defined as 1) mean personality or 2) the proportion of individuals with a certain personality type, the relationship was significant under one definition and not significant under the other.

Neither male or female group exploration or boldness composition predicted transitivity of female-female aggression networks, regardless of whether group personality composition was defined as mean personality or as the proportion of individuals with a given personality type (Tables 6 & S7). Under both definitions, transitivity of female-female aggression networks was higher in male-biased groups compared to even sex ratio groups (Mean group personality: Sum of squares = -0.979, df = -2, $p < 0.001$; Proportion of personality types: Sum of squares = -0.865, df = -2, $p = 0.001$; Tables 6 & S7).

Transitivity of female-female allopreening networks was higher when there were higher proportions of faster-exploring females (Table S7). However, mean female exploration did not predict the transitivity of female-female allopreening networks (Table 6).

iii) Group personality composition and linearity and steepness of social hierarchies.

We found that group personality composition and sex ratio did not predict the probability that male or female social hierarchies were significantly linear, regardless of whether group personality composition was defined as mean personality score or as the proportion of a given personality type (Tables 7 & S8).

Male and female group exploration and boldness composition had no effect on the steepness of male or female social hierarchies, regardless of how group personality composition was defined (Tables 7 & S8). Male social hierarchies were steeper in female-biased groups compared to even sex ratio groups, both when group personality composition was defined as mean personality score and when it was defined as the proportion of a given personality type (Mean group personality: Sum of squares = -0.335, df = -2, $p < 0.001$; Proportion of personality types: Sum of squares = -0.301, df = -2, $p < 0.001$; Tables 7 & S8). In contrast, female social hierarchies were steeper in male-biased groups compared to even sex ratio groups under both definitions (Mean group personality: Sum of squares = -0.341, df = -2, $p = 0.001$; Proportion of personality types: Sum of squares = -0.321, df = -2, $p = 0.001$; Tables 7 & S8).

Table 7. The effects of mean male exploration, mean male boldness, mean female exploration, mean female boldness, and sex ratio on the linearity and steepness of male and female dominance hierarchies. (See text for details.)

Predictor	Est. ± SE	z-value or t-value	p
Linearity Male Dominance Hierarchies			
Mean Exploration Males	3.613e-12 ± 1.099e+05	0	1
Mean Boldness Males	2.601e-11 ± 9.357e+04	0	1
Mean Exploration Females	5.260e-11 ± 9.149e+04	0	1
Mean Boldness Females	-5.854e-12 ± 1.146e+05	0	1
Sex Ratio: Male Biased	5.113e+01 ± 1.117e+05	0	1
Sex Ratio: Female Biased	-1.004e-11 ± 1.258e+05	0	1
Linearity Female Dominance Hierarchies			
Mean Exploration Males	-0.344 ± 1.486	-0.231	0.817
Mean Boldness Males	-1.947 ± 1.590	-1.225	0.221
Mean Exploration Females	-0.964 ± 1.921	-0.502	0.616
Mean Boldness Females	-1.175 ± 1.761	-0.667	0.505
Sex Ratio: Male Biased	-19.763 ± 4003.283	-0.005	0.996
Sex Ratio: Female Biased	2.403 ± 1.908	1.259	0.208
Steepness Male Dominance Hierarchies			
Mean Exploration Males	-0.054 ± 0.059	-0.900	0.382
Mean Boldness Males	0.049 ± 0.050	0.996	0.335
Mean Exploration Females	0.041 ± 0.049	0.843	0.412
Mean Boldness Females	0.104 ± 0.066	1.578	0.135
Sex Ratio: Male Biased	0.014 ± 0.064	0.214	0.833
Sex Ratio: Female Biased	0.303 ± 0.072	4.213	**0.001**
Steepness Female Dominance Hierarchies			
Mean Exploration Males	-0.100 ± 0.086	-1.166	0.263
Mean Boldness Males	0.045 ± 0.073	0.626	0.542
Mean Exploration Females	0.047 ± 0.073	0.642	0.532
Mean Boldness Females	-0.071 ± 0.094	-0.757	0.461
Sex Ratio: Male Biased	0.232 ± 0.098	2.360	**0.033**
Sex Ratio: Female Biased	-0.088 ± 0.099	-0.885	0.391

Discussion

Using 24 groups of male and female red junglefowl with varying compositions of exploration and boldness, we examined how group personality composition affected emergent group-level social dynamics. Specifically, we examined the mean number of interactions seen in groups, social network density, social network transitivity, and reciprocity, as well as the linearity and steepness of social hierarchies. Overall, our results suggest that the group personality composition of both males and females can influence emergent social dynamics, especially in terms of the frequency and network density of social interactions. Furthermore, we present evidence that some behavioural patterns in one

sex are not only influenced by the group composition of this sex but also by the group composition of the opposite sex.

We found evidence that groups with a faster female group exploration composition (i.e. groups with a higher mean and/or a higher proportion of fast exploring females) were more likely to exhibit female-female aggression, more likely to exhibit female-female allopreening, and had a lower mean number of harassment interactions. It may be the case that these findings are interrelated. The positive relationship between female group exploration composition and the occurrence of female-female allopreening may be connected to the fact that these groups were also more likely to display female-female aggression, as affiliative and aggressive interactions can reflect similar facets of social relationships (Lehmann et al. 2015). Different social mechanisms may underpin this. For example, it is possible that allopreening may serve as a method of reconciliation after bouts of aggression, that aggression may be employed by dominant birds as a mechanism to coerce allopreening from subdominant individuals, and/or that allopreening may work to foster connections between aggressed individuals. In white-faced capuchin monkeys (*Cebus capuchinus*), bonnet macaques (*Macaca radiata*), and Japanese macaques (*Macaca fuscata*), females have been shown to allogroom more with females that aggress them more compared to females that aggress them less (Silk 1982; Perry 1996; Schino et al. 2005). In Barbary macaques, dominant individuals may use aggression to coerce lower-ranking individuals to allogroom them, and subdominant individuals were shown to be more likely to groom their aggressor if the pre-aggressive social relationship with said individual was of higher quality (McFarland & Majolo 2011). Additionally, we observed a lower frequency of harassment interactions in groups where female exploration was faster; this may reflect the increased propensity for allopreening in such groups. A link between allopreening and harassment may occur if allopreening strengthens bonds between females (Radford & Du Plessis 2006; Kenny et al. 2017), and the increased social integration resulting from allopreening helps females reduce male harassment. In feral horses, social integration has been found to shelter females from harassment by males (Cameron et al. 2009). In contrast, male harassment in guppies (*Poecilia reticulata*) may lead to a lower degree

of association between females and result in females inhabiting peripheral positions in social networks (Darden et al. 2009).

Interestingly, we found that groups were more likely to exhibit female-female aggression with faster rather than slower female group exploration compositions. This was contrary to our original prediction. Given that slower-exploring females have been shown to be more likely to attain higher social status in this population (Roth et al. in Prep), and given that heightened aggression may provide a route to attaining high social status in some species (Verbeek et al. 1996; Pizzari & McDonald, 2019), we predicted that groups with a slower female group exploration composition would be more likely to exhibit female-female aggression and show higher levels of aggression. However, it is possible that with more fast-exploring females in a group, the few slow-exploring females may be more likely to behave despotically, increasing chances of aggression in such groups. In domestic fowl, Estevez et al. (2003) found that aggression was related to group size, with focal birds receiving more aggression, and giving less aggression, in larger groups compared to smaller ones. This was contrary to the authors' original prediction, and Estevez et al. (2003) hypothesize that this pattern may have arisen as a result of focal birds being a random subset of the group, due to the impracticality of observing every individual in large groups. They hypothesize that increasing group size led to a divergence of social strategies, with birds with poor fighting skills developing a tolerant (reduced aggression) strategy and a handful of skilled fighters developing a despotic (increased aggression) strategy. They hypothesize that most birds should adopt a tolerant strategy, thus explaining why the randomly chosen focal individuals gave less aggression but received more aggression in larger groups, as the success of despotic strategies may be negative frequency dependent. If the majority of individuals in a group behaved despotically, the risk of retaliation would increase, causing a decline in the net benefits related to despotism (Maynard Smith & Price, 1973; Estevez et al. 2003). In our study, when slower exploring birds were the minority, negative frequency dependence may have relaxed the costs of despotism for these individuals, making aggression more likely in groups with a faster female group exploration composition. A second possibility for our observed results has to do with the fact

that some personality types may take longer to recover from social defeat (Verbeek et al. 1999). If slower explorers take longer to recover from social defeat, they may be less likely to challenge other individuals after a social hierarchy has been established, causing aggressive interactions to be seen less in groups with a slower female group exploration composition. Although winner-loser effects were not found to predict social rank in male domestic fowl (Favati et al. 2017), it is unclear whether this pattern would hold for female red junglefowl. Lastly, it is possible that, with faster mean female exploration and/or higher proportions of fast- exploring females, females may be more likely to encounter one another simply because faster- exploring females may move more. If faster-exploring females encounter a greater number of individuals than slower-exploring females due to a proclivity for movement, faster-explorers may have more but shallower relationships than slower explorers. These social patterns may make it more difficult for faster-exploring females to remember all the individuals they encounter. Consequently, this may necessitate more frequent dominance reassessments, and thus a higher likelihood of female-female aggression, in groups with a faster female group exploration composition, compared to groups with a slower female group exploration composition. We explored this last possibility using supplemental data collected on female associations (defined as individuals being within one body length of one another; see appendix for details). We used association data rather than interaction data, as the former should provide a less biased estimate for encounter patterns. While networks were too saturated to test whether faster-exploring females had more female association partners (i.e. higher degree) than slower-exploring females, we were able to test whether faster-exploring females had weaker social bonds (i.e. lower average association strength) with other females, compared to slower-exploring females (see appendix for details). We found that an individual female's exploration did not predict her average association strength in female association networks (Table S9), providing no support for the hypothesis that faster exploring female groups were more likely to show aggression than slower exploring female groups due to faster exploring females having more, but shallower, relationships than slower explorers.

Groups with a shyer female group boldness composition were also more likely to display female-female aggression in our study. Past work has provided some evidence to suggest that shyer female red junglefowl are more likely to attain high social status in this population (Roth et al. in Prep). It may be the case that, for this behavioral trait, higher levels of aggression do correspond with high social status, explaining the finding that female-female aggression is more likely to occur in female groups with shyer compositions. Favati et al. (2017) demonstrated that, although boldness did not directly predict social rank in male domestic fowl, bolder males were more aggressive, and aggression was able to predict social status in a group setting (Favati et al. 2017). In great tits, faster explorers may also be more aggressive which may enable faster exploring juvenile males to attain dominance in pair-wise encounters (Verbeek et al. 1996; but see Dingemanse & de Goede 2004 showing this relationship may be context-dependent). In addition to the effects of female group boldness composition on female-female aggression, we found that both intersexual allopreening and male-male aggression networks were denser, and male-male aggression networks showed higher transitivity, when there were more bold females in a group. This suggests that female group boldness composition can also affect intersexual group dynamics as well as male-male group dynamics. It is important to note that the results regarding transitivity should be taken with some caution, however, as we assessed the effects of group personality composition on transitivity using linear models, despite the fact that we could not transform transitivity response variables to normality.

We found that groups with a faster female group exploration composition were more likely to exhibit male-male allopreening, have denser male-male allopreening networks, and have less dense male-male aggression networks. Interestingly, however, there was no significant difference between groups with a faster female group exploration composition and groups with a slower female group exploration composition in the mean number of male-male aggressive interactions observed. This suggests that groups with different female group exploration compositions experienced roughly the same amount of male-male aggression, but that aggression was more concentrated in terms of dyads of actors and receivers. What is curious is that female group personality composition, rather than male

group personality composition, predicted the observed social dynamics. It is possible that these results relate to the lower levels of harassment and increased likelihood of female-female allopreening seen in groups with a faster female group exploration composition. Females in groups with a faster female group exploration composition may be more socially integrated and less sexually available to males, causing more structured patterns of aggression in males (i.e. less dense networks with fewer interacting dyads but no observed difference in mean levels of male-male aggression), as males may need to compete more intensely over access to mating opportunities. Furthermore, these concentrated aggression patterns may cause male-male allopreening to be more likely and cause male-male allopreening networks to be denser, as aggression and affiliation may represent facets of the same axis. Males may also need to form stronger bonds with one another if females are more strongly bonded and less sexually available. By forming stronger bonds via allopreening, males may be able to build reproductive alliances with other males to secure access to mates. For example, male bottlenose dolphins (*Tursiops* spp.) form alliances allowing them to better compete against non-ally males for reproductive access to females (Lusseau 2007; Ermak et al. 2017). Anecdotal observations suggest that social patterns similar to such male alliances might sometimes occur in groups of feral fowl (Pizzari unpublished work).

Male-male group personality composition also influenced female-female social dynamics. Groups with a faster male group exploration composition were more likely to display female-female allopreening and expressed denser female-female allopreening networks. Similarly, groups with a shyer male group boldness composition experienced denser female-female allopreening networks. We might expect females to be more likely to allopreen or have denser allopreening networks under these conditions if male group exploration and boldness compositions predicted levels of harassment. Interestingly, however, male personality composition did not influence group-level measures of harassment, therefore, it is unlikely that male group boldness or exploration composition affected female allopreening via changes in harassment pressure. The question remains, then, as to why this pattern emerges. It is possible that fast exploring males may be more likely to spot predators if they

explore spaces more rapidly. Similarly, shy males may be more cautious and, therefore, more likely to spot predators, or they may be more wary of novel, potentially threatening, stimuli. If this is the case, groups with a faster male group exploration composition or a shyer male group boldness composition may provide better group protection, relaxing demands on female vigilance and allowing females to spend more time on other activities such as allopreening and/or allow females to allopreen with more partners. Although tradeoffs between vigilance and allopreening have yet to be studied in red junglefowl, tradeoffs between allogrooming and vigilance have been observed in a number of species (Cords 1995; Mooring & Hart 1995; Chalmeau et al. 1998; Stojan-Dolar & Heymann 2010).

Our findings suggest that, in intrasexual interactions, the group phenotypic composition of the noninteracting sex can influence emergent group properties born from interactions within the interacting sex. At an individual level, the phenotype of an individual of one sex has been shown to stimulate behaviour in an individual of the opposite sex (Mutzel et al. 2013; Roth et al. in Press). For example, in great tits, males socially paired with an older female are more likely to sire extrapair young than males paired with a younger female (Roth et al. in Press). In blue tits (*Cyanistes caeruleus*), females socially paired with a more aggressive male invest more in parental care, likely due to the lower rates of feeding by more aggressive males compared to their less aggressive counterparts (Mutzel et al. 2013). Our study demonstrates that group-level intersexual moderation of intrasexual behavior may have group-level consequences.

Although, male group personality composition did not affect any of the measures of male-male social dynamics we examined, male group personality composition did predict intersexual group dynamics. Harassment networks were denser in groups with a faster male group exploration composition, suggesting that, in general, males in these groups harassed a greater proportion of their female groupmates than did males in groups with a slower male group exploration composition. Personality has been shown to influence mate sampling in the socially monogamous great tit, with slower exploring males sampling more potential mates in the pre-breeding season than their faster exploring counterparts (Firth et al. 2018). It is possible that harassment works as a form of mate

sampling in red junglefowl, with faster exploring males sampling more females to determine which females they should invest more in, in terms of energy or ejaculate. For example, females that show more resistance to male advancement, may be less cost-effective to pursue, compared to those that show less resistance, if both potential mates are of approximately equal quality. Male group personality composition was also shown to affect intersexual allopreening networks in our study, with denser networks arising in groups with a shyer male group boldness composition. Again, if shy males are more vigilant, perhaps this allows females to allopreen with more partners, thus increasing network density, by relaxing demands on female vigilance.

Overall, female exploration composition had further reaching effects on group dynamics than did any of the other measures of group personality composition we examined, predicting six of the 24 emergent group properties we explored. Future work is needed to investigate the ecological and evolutionary consequences of the emergent group properties observed in the current study. For example, variation in likelihood or network density of allopreening could result in differential group fitness. Allopreening may reduce the prevalence of ectoparasites (de Brooke 1985; Kober & Gaston 2003; Radford & Du Plessis 2006), potentially increasing survival and reproduction of individual group members, leading to an overall increase in group-level survival and reproductive output. Higher rates of allopreening may also increase social bonding (Radford & Du Plessis 2006; Emery et al. 2007; Gill 2012; Kenny et al. 2017), which may result in benefits like more coordinated predator responses (Micheletta et al. 2012; Kern & Radford 2016; Woods et al. 2018). In common guillemots (*Uria aalge*), allopreening has been shown to increase fitness (Lewis et al. 2007). Guillemots that exhibited higher rates of within-pair allopreening, were shown to attain higher mean reproductive success, across the years where the two individuals bred as a pair (Lewis et al. 2007). Furthermore, pairs that displayed higher rates of allopreening with neighboring breeding pairs, were more likely to fledge a chick in the current breeding season (Lewis et al. 2007). Similarly, in primates, allogrooming may increase fitness by reducing ectoparasites, strengthening social relationships, and decreasing stress (Seyfarth & Cheney 1984; Boccia et al. 1989; Dunbar 1991; Tanaka & Takefushi 1993; Aureli et al.

1999; Henazi & Barrett 1999; Wittig et al. 2008; Silk et al. 2009; 2010; Tiddi et al. 2012; McFarland & Majolo 2013). In contrast, increased connectivity in interaction networks could result in a higher spread of pathogens, by bringing more individuals in close spatial proximity with one another, thereby reducing group fitness (Cross et al. 2004; Naug 2008).

In addition to shedding light on patterns of disease transmission, social network analyses can help scientists understand processes such as information flow, formation of social hierarchies, collective movement, and much more, making the adoption of this rapidly growing technique integral to unraveling the causes and consequences of complex social patterns (reviewed in Pinter-Wollman et al. 2013). Our study was unique in that it explored how the individual phenotypic makeup of a group affected the groups' social network structure. In general, studies exploring intergroup variation in social network structure are limited, and those that exist focus primarily on environmental drivers, comparing populations of similar species exposed to different environmental conditions (e.g. predator density, resource availability), rather than examining the effects of group phenotypic composition (Sundaresan et al. 2007; Kasper & Voelkl 2009; de Silva & Wittemyer 2012; Pinter-Wollman et al. 2013).

Examining how emergent group social patterns and structure are affected by the mean personality of a group (and/or the proportion of individuals of a certain personality type) has seldom been done and represents an important first step in understanding how the personalities of individuals in a group can work together to shape group-level processes that may in turn feedback to affect individual level performance. However, it is also possible that other aspects of group personality composition, such as variance in personality measures, may be important predictors of emergent social patterns and structure. For example, although we did not find evidence that the steepness or linearity of same sex social hierarchies was predicted by the mean exploration or boldness of either sex, it is possible that variance in personality types may predict social hierarchy structure. Furthermore, with respect to linearity, we were limited to analyzing whether group personality composition could predict whether hierarchies were significantly linear or not. It is possible that within groups where hierarchies

were significantly linear, mean personality may have predicted how linear hierarchies were, but unfortunately our sample size was not large enough to test this. Future work should examine this possibility in addition to exploring the effects of other measures of group personality composition, such as variance.

In conclusion, our study contributes to elucidating the effects of group phenotypic composition on emergent group dynamics. We demonstrate that the group phenotypic composition of one sex can influence intrasexual group dynamics born from interactions of the opposite sex. We advocate that more studies should focus on disentangling the relationship between group phenotypic composition and social network structure, as doing so will help illustrate how the individual phenotypic makeup of a group, that potentially arises as a result of social processes (Wolf et al. 2007; Dingemanse & Wolf 2010; Wolf & Weissing 2010), feeds back onto group-level emergent properties.

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Supplementary Information

Follow-up analysis testing whether female exploration predicts the strength of female-female associations.

We used association data collected from scan samples where individuals that were within one body length of one another were considered to be associated, and those that were not within one body length of one another were not considered to be associated. We conducted scan samples every half hour during group observations, resulting in a total of 77 scan samples for each of the 24 replicate groups. We constructed networks based on female-female associations and used this to calculate average association strengths for individual females. We computed average association strength as the total number of associations a female displayed divided by the number of unique females she associated with (each time a female was recorded as associating with another female was counted as one association, and a female could be associated with multiple female group mates at any given time). We ran a linear mixed model with average association strength as the response. We included female exploration and group sex ratio as fixed effects and individual identity and group identity as random effects. We found that a female's exploration score did not predict her average association strength, but we found that females had higher average association strengths in female-biased groups compared to even sex ratio groups (Table S8). We constructed 1000 randomized networks using node permutations and calculated 1000 average association strength values for each individual, based on these randomized networks. We compared our observed t-value for the female biased sex ratio to the distribution of randomized t-values for the female biased sex ratio and found that our observed t-value was significantly different from the randomized distribution ($p < 0.001$). Furthermore, a likelihood-ratio test suggested that the overall effect of sex ratio on average association strength was significant (Chi-squared = 13.453, df = 2, $p = 0.001$).

Table S1. Summary statistics for emergent group properties related to harassments, male-male ("M-M") aggressions, female-female ("F-F") aggressions, male-male ("M-M") allopreening, female-female ("F-F") allopreening, and intersexual allopreening, as well as the steepness of male and female dominance hierarchies, for all observed groups, male-biased groups, even sex ratio groups, and female-biased groups.

	Mean ± SD All Groups	**Range All Groups**	**Mean ± SD Male-Biased Groups**	**Range Male-Biased Groups**	**Mean ± SD Even Sex Ratio Groups**	**Range Even Sex Ratio Groups**	**Mean ± SD Female-Biased Groups**	**Range Female-Biased Groups**
Mean Number								
Harassments	4.356 ± 4.658	0.111 - 34.333	7.458 ± 6.215	0.667 - 34.333	3.888 ± 2.781	0.667 - 14.667	1.722 ± 1.499	0.111 - 9.111
M-M Aggressions	5.814 ± 4.748	0.167 - 32.667	4.271 ± 2.228	0.889 - 10.667	4.989 ± 2.678	0.167 - 11.167	8.182 ± 6.875	0.333 - 32.667
F-F Aggressions	1.593 ± 1.606	0 - 8.667	1.117 ± 1.564	0 – 7.667	1.146 ± 0.922	0 - 5.500	2.516 ± 1.792	0 – 8.667
M-M Allopreening	0.065 ± 0.187	0 - 1.667	0.177 ± 0.287	0 – 1.667	0.013 ± 0.052	0 - 0.333	0.004 ± 0.036	0 – 0.333
F-F Allopreening	0.447 ± 0.638	0 – 5.000	0.386 ± 0.651	0 – 3.000	0.453 ± 0.739	0 – 5.000	0.503 ± 0.503	0 – 2.778
Intersexual Allopreening	0.258 ± 0.389	0 – 2.500	0.363 ± 0.378	0 – 1.583	0.134 ± 0.246	0 - 1.417	0.277 ± 0.475	0 – 2.500
Network Density								
Harassments	0.856 ± 0.110	0.630 - 1.000	0.880 ± 0.104	0.667 - 1.000	0.819 ± 0.110	0.667 - 0.972	0.870 ± 0.119	0.630 - 1.000
M-M Aggressions	0.714 ± 0.166	0.458 - 1.000	0.646 ± 0.111	0.458 - 0.792	0.683 ± 0.161	0.467 - 0.933	0.813 ± 0.188	0.500 - 1.000
F-F Aggressions	0.458 ± 0.113	0.167 - 0.667	0.438 ± 0.177	0.167 - 0.667	0.467 ± 0.056	0.400- 0.533	0.469 ± 0.083	0.333 - 0.625
M-M Allopreening	0.053 ± 0.067	0 - 0.222	0.109 ± 0.067	0.014 - 0.222	0.029 ± 0.038	0 - 0.100	0.021 ± 0.059	0 – 0.167
F-F Allopreening	0.368 ± 0.182	0 - 0.667	0.479 ± 0.243	0 – 0.667	0.338 ± 0.131	0.167 - 0.567	0.288 ± 0.099	0.167 - 0.472
Intersexual Allopreening	0.233 ± 0.147	0.037 - 0.593	0.319 ± 0.133	0.111 - 0.444	0.146 ± 0.054	0.042 - 0.194	0.234 ± 0.181	0.037 - 0.593
Network Transitivity								
M-M Aggressions	0.943 ± 0.077	0.745 - 1.000	0.900 ± 0.090	0.745 - 1.000	0.928 ± 0.074	0.789 - 1.000	1.000 ± 0	1.000 – 1.000
F-F Aggressions	0.893 ± 0.112	0.635 - 1.000	1.000 ± 0	1.000 – 1.000	0.858 ± 0.113	0.730 - 1.000	0.849 ± 0.106	0.635 - 0.947
F-F Allopreening	0.498 ± 0.344	0 – 1.000	0.571 ± 0.535	0 – 1.000	0.311 ± 0.224	0 - 0.600	0.620 ± 0.124	0.429 - 0.786
Reciprocity								
F-F Allopreening	0.501 ± 0.232	0 - 0.824	0.381 ± 0.267	0 – 0.667	0.640 ± 0.170	0.400 - 0.824	0.466 ± 0.202	0.111 - 0.667
Intersexual Allopreening	0.253 ± 0.200	0 - 0.632	0.405 ± 0.143	0.167 - 0.632	0.117 ± 0.160	0 - 0.462	0.236 ± 0.194	0 – 0.563
Steepness								
Male Hierarchies	0.738 ± 0.183	0.458 - 1.196	0.628 ± 0.119	0.469 - 0.859	0.638 ± 0.121	0.458 - 0.820	0.924 ± 0.119	0.796 - 1.196
Female Hierarchies	0.674 ± 0.197	0.346 - 0.967	0.892 ± 0.090	0.720 - 0.967	0.602 ± 0.145	0.449 - 0.872	0.573 ± 0.171	0.346 - 0.783

Table S2. The effects of the proportion of fast exploring males, the proportion of bold males, the proportion of fast exploring females, the proportion of bold females, and sex ratio on the mean number of harassments, mean number of male-male aggressive interactions, whether female-female aggression occurred, and the mean number of female-female aggressive interactions that occurred when female-female aggression was observed. (See text for details.)

Predictor	Est. ± SE	z-value	p
Harassment: Mean			
Proportion Fast Exploring Males	0.251 ± 0.463	0.541	0.588
Proportion Bold Males	0.095 ± 0.301	0.316	0.752
Proportion Fast Exploring Females	-1.210 ± 0.488	-2.479	**0.013**
Proportion Bold Females	-0.075 ± 0.326	-0.230	0.818
Sex Ratio: Male Biased	0.719 ± 0.166	4.322	**<0.001**
Sex Ratio: Female Biased	-0.741 ± 0.184	-4.013	**<0.001**
Male-Male Aggression: Mean			
Proportion Fast Exploring Males	0.094 ± 0.513	0.183	0.855
Proportion Bold Males	-0.047 ± 0.327	-0.142	0.887
Proportion Fast Exploring Females	-0.170 ± 0.495	-0.344	0.731
Proportion Bold Females	0.197 ± 0.330	0.598	0.550
Sex Ratio: Male Biased	-0.111 ± 0.162	-0.689	0.491
Sex Ratio: Female Biased	0.429 ± 0.174	2.458	**0.014**$^{+}$
Female-Female Aggression: Binary			
Proportion Fast Exploring Males	-1.253 ± 3.281	-0.382	0.703^{++}
Proportion Bold Males	0.895 ± 1.999	0.448	0.654^{++}
Proportion Fast Exploring Females	6.908 ± 3.002	2.301	**0.021**
Proportion Bold Females	-5.105 ± 2.054	-2.486	**0.013**
Sex Ratio: Male Biased	-3.436 ± 0.883	-3.892	**<0.001**
Sex Ratio: Female Biased	0.424 ± 1.440	0.294	0.769
Female-Female Aggression: Mean			
Proportion Fast Exploring Males	-0.475 ± 0.560	-0.849	0.396
Proportion Bold Males	0.091 ± 0.378	0.242	0.809
Proportion Fast Exploring Females	0.021 ± 0.699	0.030	0.976
Proportion Bold Females	-0.505 ± 0.471	-1.071	0.284
Sex Ratio: Male Biased	-0.013 ± 0.250	-0.052	0.958
Sex Ratio: Female Biased	0.695 ± 0.255	2.724	**0.006**

"+" denotes that when group personality composition was defined as 1) mean personality or 2) the proportion of individuals with a certain personality type, the relationship was significant under one definition and marginally non-significant ($p < 0.10$) under the other definition. In contrast, "++" denotes that the relationship was significant under one definition and not significant under the other.

Table S3. The effects of the proportion of fast exploring males, the proportion of bold males, the proportion of fast exploring females, the proportion of bold females, and sex ratio on the occurrence of male-male allopreening, the occurrence of female-female allopreening, the mean number of female-female allopreening interactions that occurred when female-female allopreening was observed, the occurrence of intersexual allopreening, and the mean number of intersexual allopreening interactions that occurred when female-female allopreening was observed. (See text for details.)

Predictor	Est. ± SE	z-value	p
Male-Male Allopreening: Binary			
Proportion Fast Exploring Males	-1.659 ± 1.791	-0.926	0.354
Proportion Bold Males	-1.730 ± 1.319	-1.312	0.190
Proportion Fast Exploring Females	4.092 ± 1.487	2.751	**0.006**
Proportion Bold Females	0.036 ± 0.934	0.039	0.969
Sex Ratio: Male Biased	2.973 ± 0.536	5.546	**<0.001**
Sex Ratio: Female Biased	-1.934 ± 1.130	-1.711	0.087
Female-Female Allopreening: Binary			
Proportion Fast Exploring Males	4.288 ± 1.533	2.797	**0.005**$^{+}$
Proportion Bold Males	-1.959 ± 0.845	-2.319	**0.020**$^{++}$
Proportion Fast Exploring Females	4.291 ± 1.420	3.022	**0.003**$^{+}$
Proportion Bold Females	0.707 ± 0.852	0.830	0.406
Sex Ratio: Male Biased	-0.559 ± 0.395	-1.414	0.157
Sex Ratio: Female Biased	2.349 ± 0.507	4.633	**<0.001**
Female-Female Allopreening: Mean			
Proportion Fast Exploring Males	0.576 ± 0.587	0.982	0.326
Proportion Bold Males	-0.587 ± 0.378	-1.550	0.121
Proportion Fast Exploring Females	0.128 ± 0.625	0.204	0.838
Proportion Bold Females	0.212 ± 0.380	0.558	0.577
Sex Ratio: Male Biased	0.114 ± 0.201	0.567	0.571
Sex Ratio: Female Biased	-0.154 ± 0.199	-0.774	0.439
Intersexual Allopreening: Binary			
Proportion Fast Exploring Males	1.010 ± 1.857	0.544	0.587
Proportion Bold Males	-1.040 ± 1.220	-0.853	0.394
Proportion Fast Exploring Females	2.345 ± 1.942	1.208	0.227
Proportion Bold Females	2.361 ± 1.462	1.616	0.106
Sex Ratio: Male Biased	1.969 ± 0.685	2.876	**0.004**
Sex Ratio: Female Biased	1.023 ± 0.643	1.591	0.112
Intersexual Allopreening: Mean			
Proportion Fast Exploring Males	-0.319 ± 0.943	-0.338	0.736
Proportion Bold Males	-0.436 ± 0.602	-0.724	0.469
Proportion Fast Exploring Females	-0.134 ± 0.886	-0.151	0.880
Proportion Bold Females	0.639 ± 0.581	1.099	0.272
Sex Ratio: Male Biased	0.697 ± 0.292	2.384	**0.017**
Sex Ratio: Female Biased	0.353 ± 0.318	1.108	0.268

"+" denotes that when group personality composition was defined as 1) mean personality or 2) the proportion of individuals with a certain personality type, the relationship was significant under one definition and marginally non-significant ($p < 0.10$) under the other definition. In contrast, "++" denotes that the relationship was significant under one definition and not significant under the other.

Table S4. The effects of the proportion of fast exploring males, the proportion of bold males, the proportion of fast exploring females, the proportion of bold females, and sex ratio on harassment, male-male aggression, and female-female aggression network densities. (See text for details.)

Predictor	Est. ± SE	z-value	p
Harassment			
Proportion Fast Exploring Males	1.398 ± 0.829	1.686	0.092^{+}
Proportion Bold Males	-0.369 ± 0.538	-0.687	0.492
Proportion Fast Exploring Females	-1.810 ± 0.938	-1.930	0.054
Proportion Bold Females	0.622 ± 0.581	1.070	0.285
Sex Ratio: Male Biased	0.710 ± 0.292	2.435	**0.015**
Sex Ratio: Female Biased	0.709 ± 0.295	2.401	**0.016**
Male-Male Aggression			
Proportion Fast Exploring Males	-1.482 ± 0.695	-2.132	**0.03**3^{++}
Proportion Bold Males	0.329 ± 0.411	0.800	0.424
Proportion Fast Exploring Females	-1.302 ± 0.555	-2.347	**0.019**
Proportion Bold Females	1.197 ± 0.354	3.384	**0.001**
Sex Ratio: Male Biased	-0.035 ± 0.170	-0.204	0.839
Sex Ratio: Female Biased	0.802 ± 0.408	1.966	**0.049**
Female-Female Aggression			
Proportion Fast Exploring Males	-0.491 ± 0.531	-0.925	0.355
Proportion Bold Males	0.455 ± 0.370	1.232	0.218
Proportion Fast Exploring Females	-0.615 ± 0.614	-1.002	0.317
Proportion Bold Females	0.071 ± 0.521	0.136	0.892
Sex Ratio: Male Biased	-0.109 ± 0.325	-0.337	0.736
Sex Ratio: Female Biased	-0.050 ± 0.182	-0.273	0.785

"+" denotes that when group personality composition was defined as 1) mean personality or 2) the proportion of individuals with a certain personality type, the relationship was significant under one definition and marginally non-significant ($p < 0.10$) under the other definition. In contrast, "++" denotes that the relationship was significant under one definition and not significant under the other.

Table S5. The effects of the proportion of fast exploring males, the proportion of bold males, the proportion of fast exploring females, the proportion of bold females, and sex ratio on male-male allopreening, female-female allopreening, and intersexual network densities. (See text for details.)

Predictor	Est. ± SE	z-value	p
Male-Male Allopreening			
Proportion Fast Exploring Males	0.078 ± 1.519	0.052	0.959
Proportion Bold Males	-0.078 ± 0.841	-0.093	0.926
Proportion Fast Exploring Females	3.653 ± 1.116	3.274	**0.001**
Proportion Bold Females	-0.707 ± 0.642	-1.101	0.271^{++}
Sex Ratio: Male Biased	1.168 ± 0.422	2.770	**0.006**
Sex Ratio: Female Biased	-0.686 ± 1.099	-0.624	0.533
Female-Female Allopreening			
Proportion Fast Exploring Males	2.738 ± 0.581	4.710	**<0.001**
Proportion Bold Males	-1.503 ± 0.408	-3.684	**<0.001**
Proportion Fast Exploring Females	-0.022 ± 0.685	-0.032	0.974
Proportion Bold Females	-0.260 ± 0.554	-0.468	0.640
Sex Ratio: Male Biased	0.664 ± 0.332	2.001	**0.045**$^{+}$
Sex Ratio: Female Biased	0.117 ± 0.201	0.579	0.563
Intersexual Allopreening			
Proportion Fast Exploring Males	-0.251 ± 0.521	-0.481	0.630
Proportion Bold Males	-0.582 ± 0.336	-1.733	0.083^{+}
Proportion Fast Exploring Females	-0.245 ± 0.485	-0.506	0.613^{++}
Proportion Bold Females	0.967 ± 0.322	2.998	**0.003**
Sex Ratio: Male Biased	1.126 ± 0.161	6.999	**<0.001**
Sex Ratio: Female Biased	0.790 ± 0.182	4.350	**<0.001**

"+" denotes that when group personality composition was defined as 1) mean personality or 2) the proportion of individuals with a certain personality type, the relationship was significant under one definition and marginally non-significant ($p < 0.10$) under the other definition. In contrast, "++" denotes that the relationship was significant under one definition and not significant under the other.

Table S6. The effects of the proportion of fast exploring males, the proportion of bold males, the proportion of fast exploring females, the proportion of bold females, and sex ratio on reciprocity in female-female allopreening and intersexual allopreening networks. (See text for details.)

Predictor	Est. ± SE	t-value	p
Female-Female Allopreening			
Proportion Fast Exploring Males	0.005 ± 0.362	0.015	0.988
Proportion Bold Males	-0.127 ± 0.220	-0.578	0.571
Proportion Fast Exploring Females	0.600 ± 0.367	1.636	0.121
Proportion Bold Females	0.187 ± 0.221	0.845	0.410
Sex Ratio: Male Biased	-0.269 ± 0.113	-2.390	**0.030**$^{+}$
Sex Ratio: Female Biased	-0.161 ± 0.117	-1.376	0.188
Intersexual Allopreening			
Proportion Fast Exploring Males	-0.176 ± 0.255	-0.690	0.500
Proportion Bold Males	-0.037 ± 0.162	-0.229	0.822
Proportion Fast Exploring Females	0.310 ± 0.245	1.263	0.224
Proportion Bold Females	0.361 ± 0.163	2.210	**0.041**$^{++}$
Sex Ratio: Male Biased	0.322 ± 0.080	4.026	**0.001**
Sex Ratio: Female Biased	0.143 ± 0.086	1.660	0.115

"+" denotes that when group personality composition was defined as 1) mean personality or 2) the proportion of individuals with a certain personality type, the relationship was significant under one definition and marginally non-significant ($p < 0.10$) under the other definition. In contrast, "++" denotes that the relationship was significant under one definition and not significant under the other.

Table S7. The effects of the proportion of fast exploring males, the proportion of bold males, the proportion of fast exploring females, the proportion of bold females, and sex ratio on male-male aggression, female-female aggression, and female-female allopreening network transitivity. (See text for details.)

Predictor	Est. ± SE	t-value	p
Male-Male Aggression			
Proportion Fast Exploring Males	-0.285 ± 0.326	-0.875	0.394
Proportion Bold Males	-0.122 ± 0.208	-0.588	0.564
Proportion Fast Exploring Females	0.139 ± 0.314	0.444	0.663
Proportion Bold Females	0.539 ± 0.209	2.575	**0.020**
Sex Ratio: Male Biased	-0.027 ± 0.102	-0.260	0.798
Sex Ratio: Female Biased	0.358 ± 0.110	3.243	**0.005**
Female-Female Aggression			
Proportion Fast Exploring Males	-0.224 ± 0.413	-0.544	0.595
Proportion Bold Males	-0.024 ± 0.275	-0.087	0.932
Proportion Fast Exploring Females	-0.076 ± 0.424	-0.179	0.860
Proportion Bold Females	-0.041 ± 0.296	-0.140	0.891
Sex Ratio: Male Biased	0.434 ± 0.149	2.904	**0.011**
Sex Ratio: Female Biased	-0.079 ± 0.140	-0.566	0.580
Female-Female Allopreening			
Proportion Fast Exploring Males	0.525 ± 0.530	0.990	0.337
Proportion Bold Males	0.399 ± 0.322	1.238	0.234
Proportion Fast Exploring Females	1.184 ± 0.537	2.204	**0.043**$^{++}$
Proportion Bold Females	0.114 ± 0.325	0.352	0.730
Sex Ratio: Male Biased	0.210 ± 0.165	1.269	0.223
Sex Ratio: Female Biased	0.219 ± 0.171	1.281	0.219

"++" denotes that when group personality composition was defined as 1) mean personality or 2) the proportion of individuals with a certain personality type, the relationship was significant under one definition and not significant under the other.

Table S8. The effects of the proportion of fast exploring males, the proportion of bold males, the proportion of fast exploring females, the proportion of bold females, and sex ratio on the linearity and steepness of male and female dominance hierarchies. (See text for details.)

Predictor	Est. ± SE	z-value or t-value	p
Linearity Male Dominance Hierarchies			
Proportion Fast Exploring Males	1.428e-10 ± 3.545e+05	0	1
Proportion Bold Males	-9.621e-13 ± 2.258e+05	0	1
Proportion Fast Exploring Females	4.199e-10 ± 3.415e+05	0	1
Proportion Bold Females	6.816e-10 ± 2.276e+05	0	1
Sex Ratio: Male Biased	5.113e+01 ± 1.113e+05	0	1
Sex Ratio: Female Biased	6.138e-11 ± 1.199e+05	0	1
Linearity Female Dominance Hierarchies			
Proportion Fast Exploring Males	-2.043 ± 5.029	-0.406	0.685
Proportion Bold Males	-6.194 ± 4.404	-1.406	0.160
Proportion Fast Exploring Females	-5.454 ± 7.494	-0.728	0.467
Proportion Bold Females	-2.635 ± 5.933	-0.444	0.657
Sex Ratio: Male Biased	-20.136 ± 3906.087	-0.005	0.996
Sex Ratio: Female Biased	3.251 ± 2.148	1.514	0.130
Steepness Male Dominance Hierarchies			
Proportion Fast Exploring Males	-0.252 ± 0.194	-1.298	0.214
Proportion Bold Males	0.133 ± 0.125	1.067	0.303
Proportion Fast Exploring Females	-0.055 ± 0.185	-0.296	0.771
Proportion Bold Females	0.241 ± 0.124	1.939	0.072
Sex Ratio: Male Biased	0.010 ± 0.065	0.157	0.878
Sex Ratio: Female Biased	0.279 ± 0.071	3.919	**0.001**
Steepness Female Dominance Hierarchies			
Proportion Fast Exploring Males	-0.142 ± 0.266	-0.534	0.602
Proportion Bold Males	0.044 ± 0.181	0.242	0.812
Proportion Fast Exploring Females	0.171 ± 0.272	0.627	0.541
Proportion Bold Females	-0.048 ± 0.192	-0.249	0.807
Sex Ratio: Male Biased	0.258 ± 0.101	2.561	**0.023**
Sex Ratio: Female Biased	-0.058 ± 0.096	-0.609	0.552

Table S9. The effects of focal female exploration and group sex ratio on a female's average association strength in female association networks where two females were considered to be associated if they were ≤ one body length apart during scan samples. (See text for details.)

Predictor	Est. ± SE	df	t-value	p
Proportion Fast Exploring Males	0.010 ± 0.028	26.539	0.349	0.730
Sex Ratio: Male Biased	0.206 ± 0.170	15.841	1.210	0.244
Sex Ratio: Female Biased	-0.474 ± 0.169	11.595	-2.805	0.016

Figure S1. Graphs of harassment networks. Arrows point from the actor to the receiver. Blue circles represent males and pink circles represent females. Network graphs contained in the blue rectangle are from male-biased groups, network graphs contained in the green rectangle are from even sex ratio groups, and network graphs contained in the red rectangle are from female-biased groups.

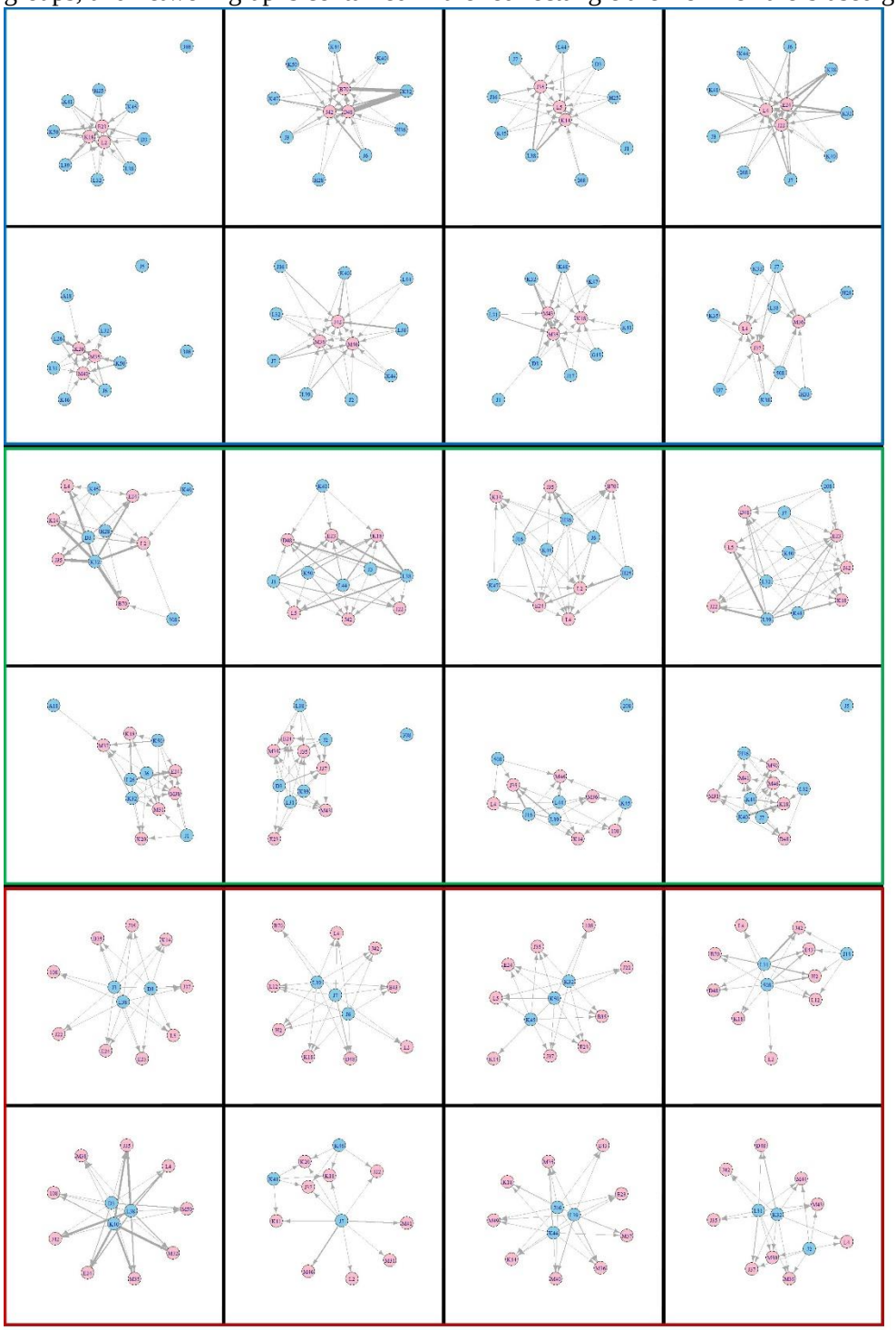


Figure S2. Graphs of male-male aggression networks. Arrows point form the actor to the receiver. Blue circles represent males and pink circles represent females. Network graphs contained in the blue rectangle are from male-biased groups, network graphs contained in the green rectangle are from even sex ratio groups, and network graphs contained in the red rectangle are from female-biased groups.

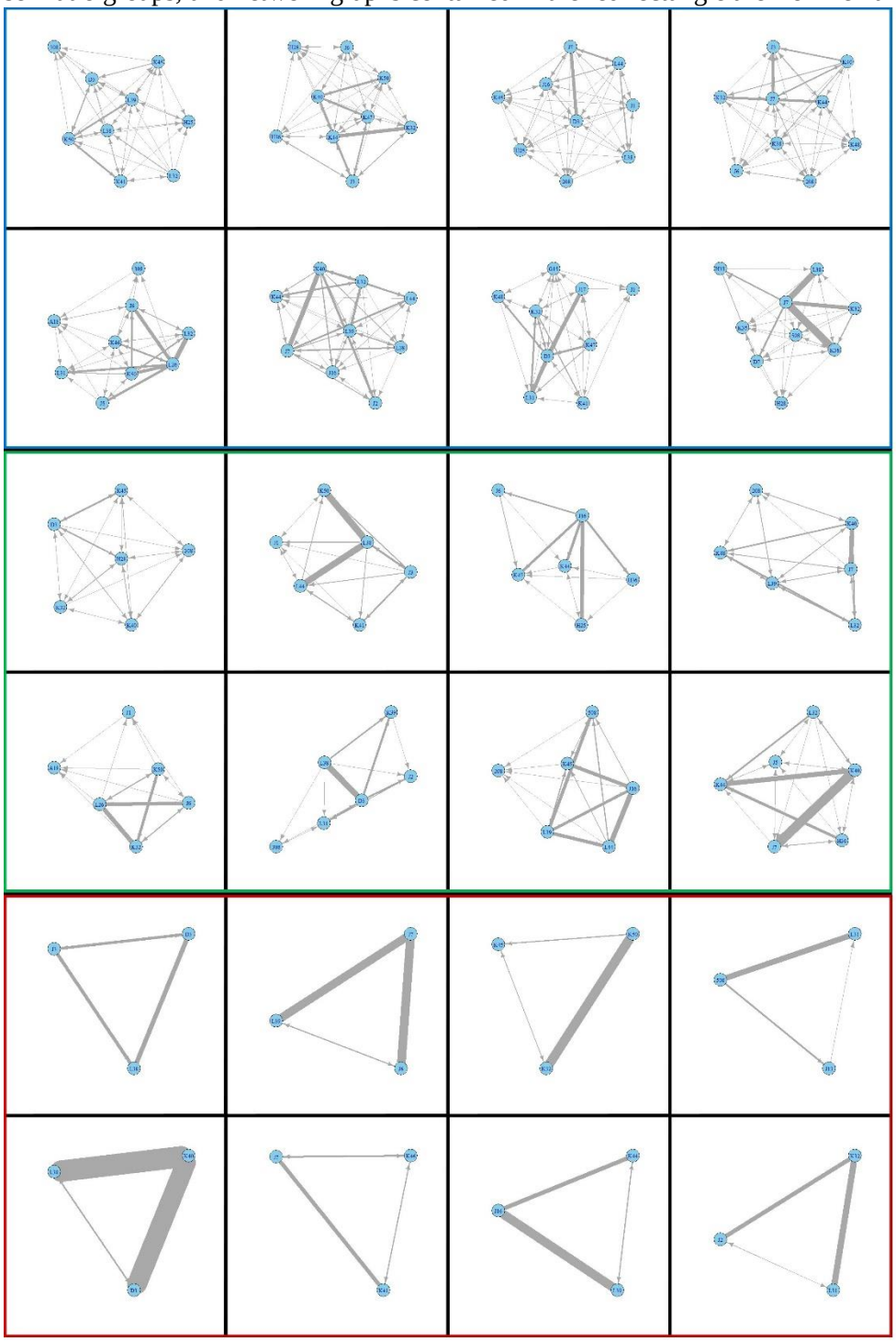


Figure S3. Graphs of female-female aggression networks. Arrows point form the actor to the receiver. Blue circles represent males and pink circles represent females. Network graphs contained in the blue rectangle are from male-biased groups, network graphs contained in the green rectangle are from even sex ratio groups, and network graphs contained in the red rectangle are from female-biased groups.

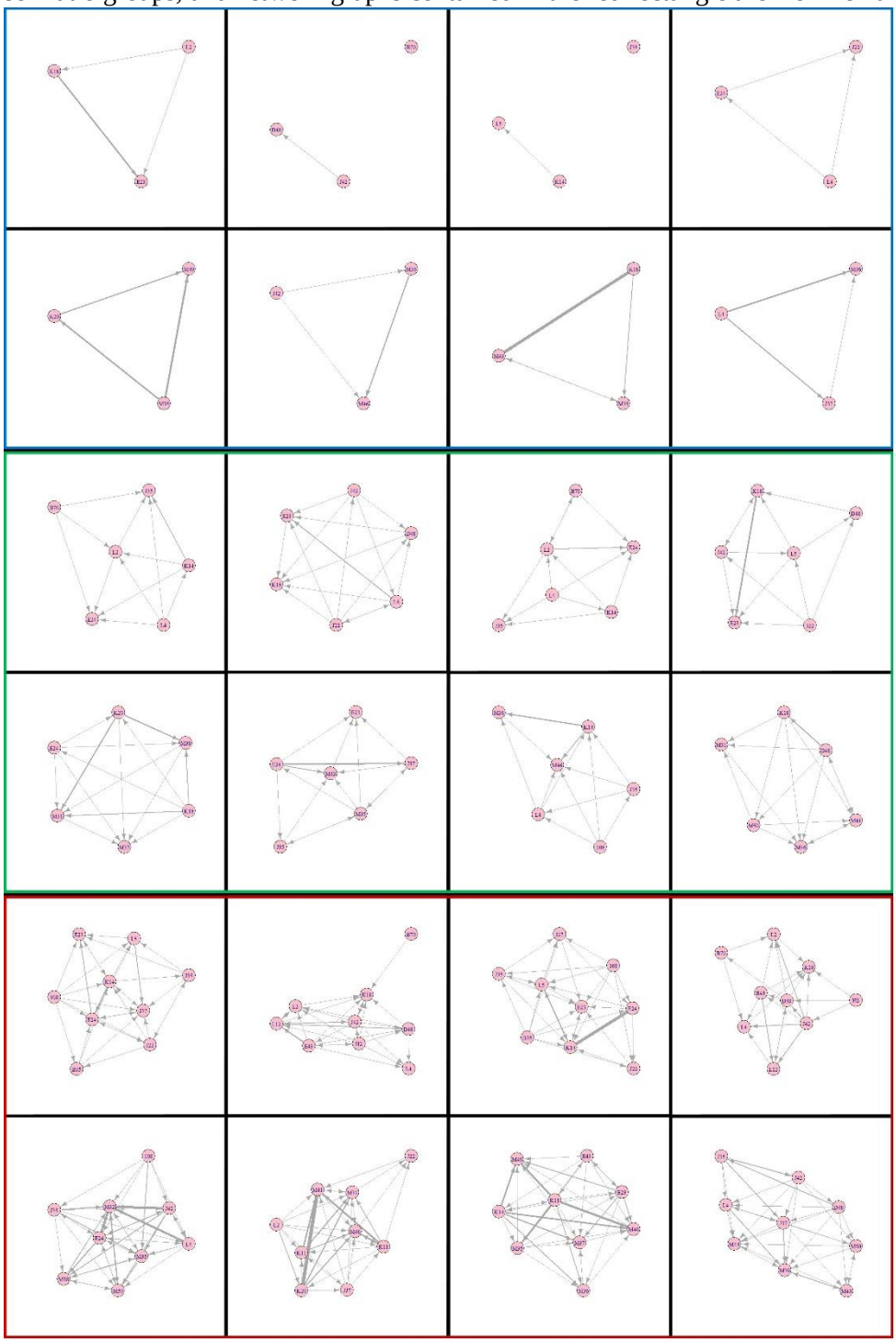


Figure S4. Graphs of male-male allopreening networks. Arrows point form the actor to the receiver. Blue circles represent males and pink circles represent females. Network graphs contained in the blue rectangle are from male-biased groups, network graphs contained in the green rectangle are from even sex ratio groups, and network graphs contained in the red rectangle are from female-biased groups.

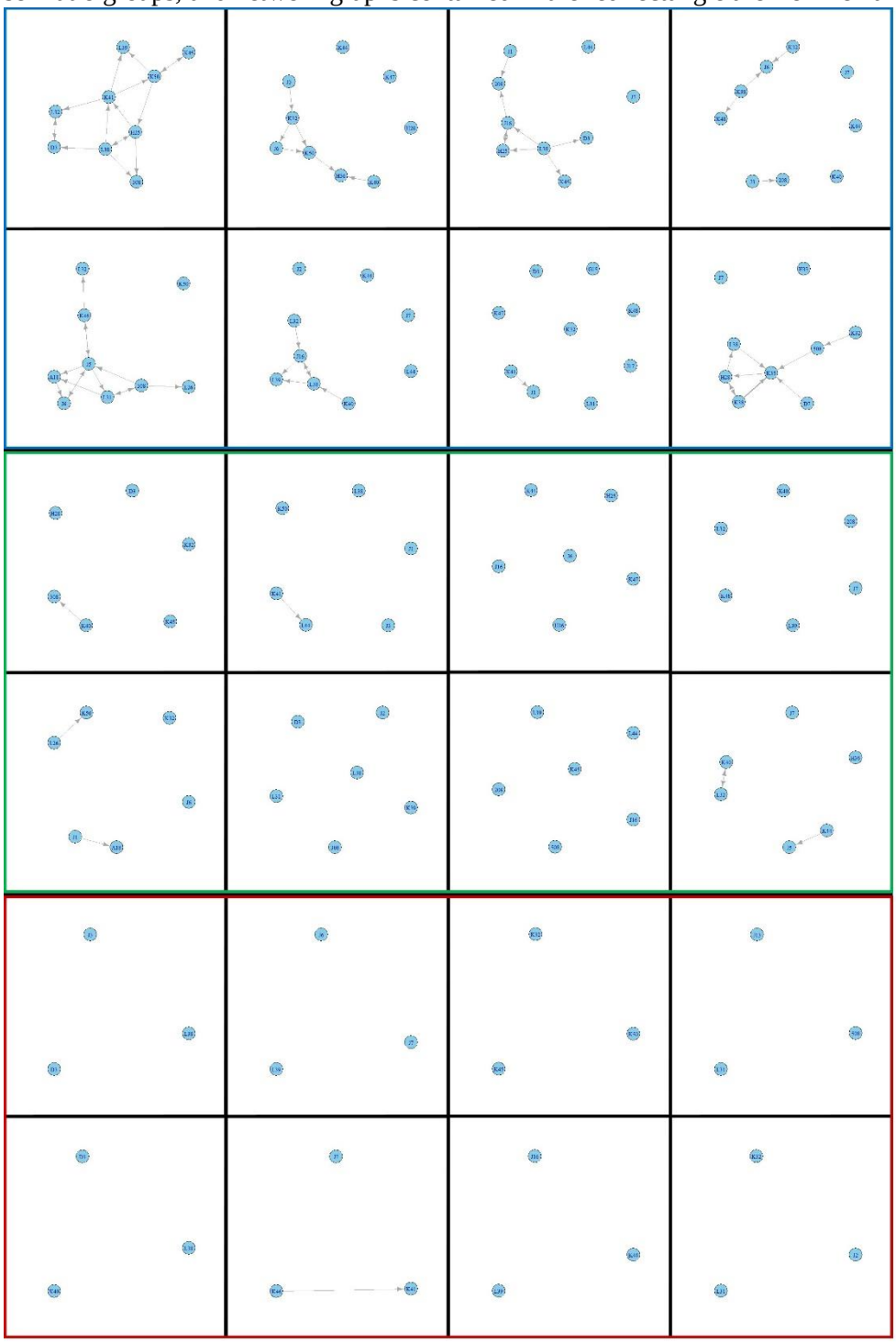


Figure S5. Graphs of female-female allopreening networks. Arrows point form the actor to the receiver. Blue circles represent males and pink circles represent females. Network graphs contained in the blue rectangle are from male-biased groups, network graphs contained in the green rectangle are from even sex ratio groups, and network graphs contained in the red rectangle are from female-biased groups.

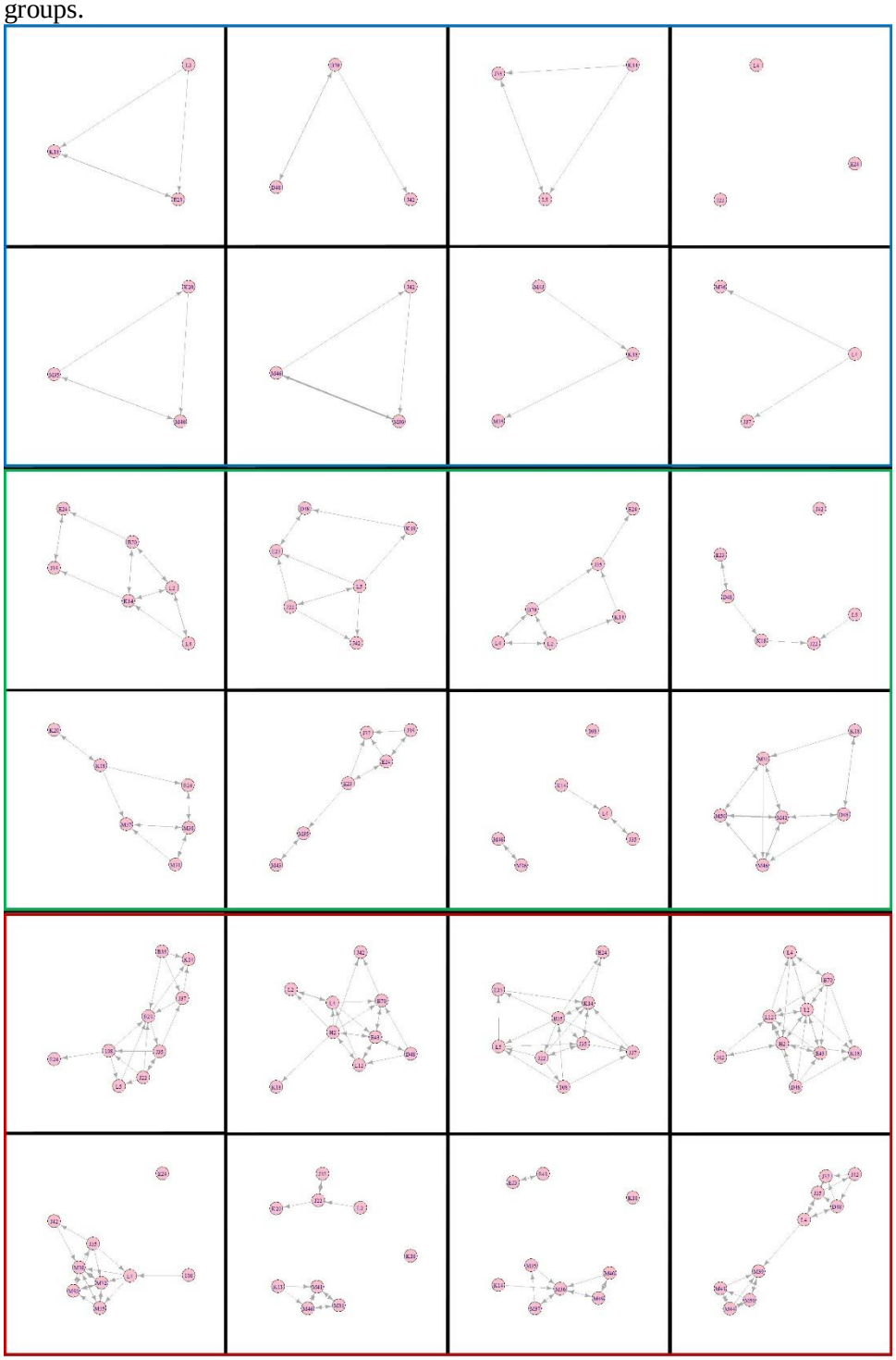
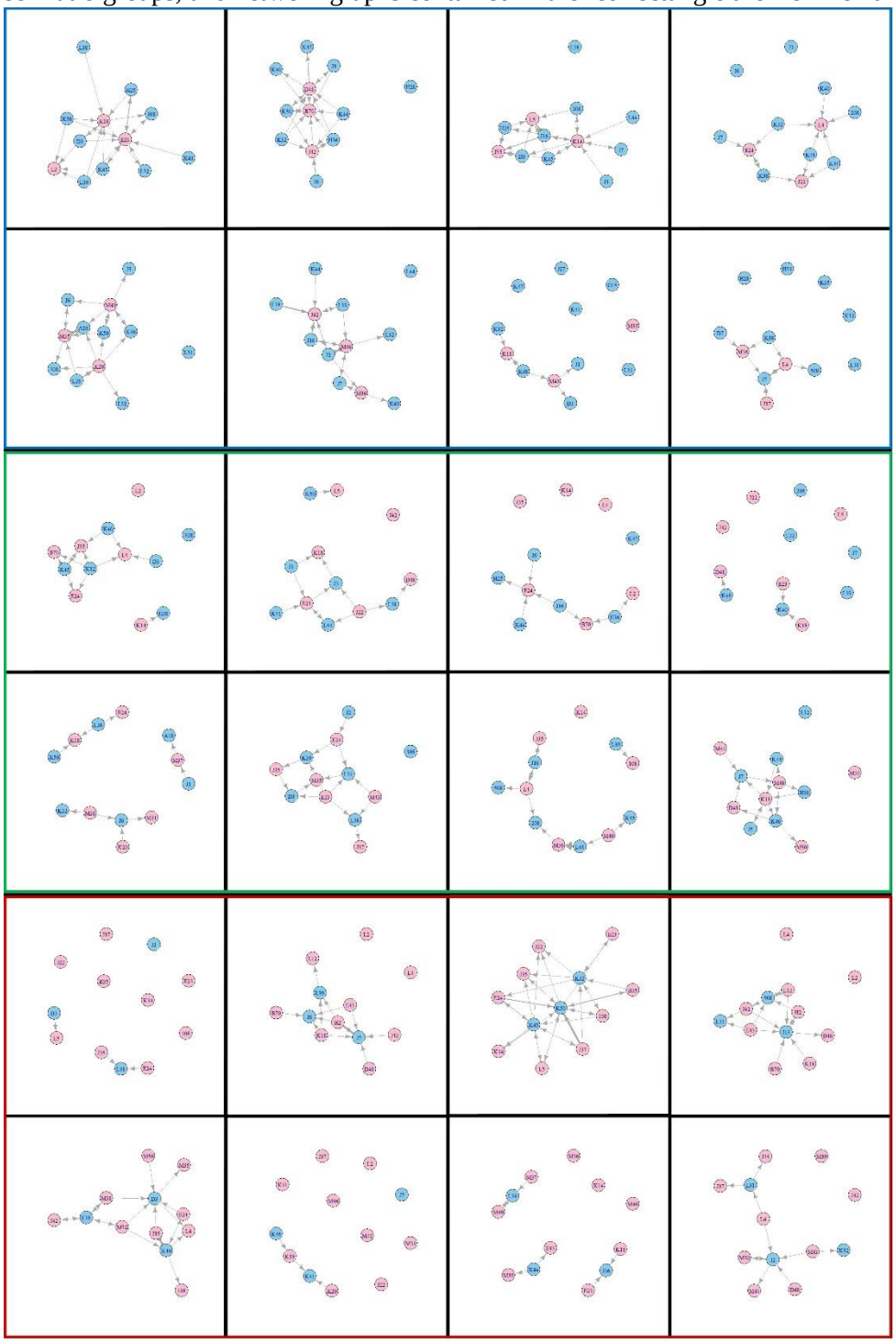


Figure S6. Graphs of intersexual allopreening networks. Arrows point form the actor to the receiver. Blue circles represent males and pink circles represent females. Network graphs contained in the blue rectangle are from male-biased groups, network graphs contained in the green rectangle are from even sex ratio groups, and network graphs contained in the red rectangle are from female-biased groups.



Chapter 6

General Discussion

GENERAL DISCUSSION

Aims and Motivation

The primary aim of my thesis was to explore the effects of animal personality in a social context, examining both individual and group level consequences of interindividual behavioral variation. This investigation was prompted by previous work suggesting that animal personality may affect reproductive encounters, aggressive interactions, social learning, and general patterns of associations (e.g. Pike et al. 2008; Matessi et al. 2010; Schuett et al. 2010; Aplin et al. 2012; 2013). This thesis was further motivated by the fact that, although numerous studies have demonstrated the fitness effects of an individual's personality (reviewed in Dingemanse & Réale 2005; Smith & Blumstein 2008), 1) few have explored how the social environment may modulate relationships between focal personality and reproductive performance, and 2) limited work has been conducted to examine how the personality composition of a group affects group level dynamics. My thesis helps fill these existing gaps in knowledge using a dual study system of wild great tits (*Parus major*) and captive red junglefowl (*Gallus gallus*). Furthermore, my thesis attempts to understand the driving mechanisms behind the maintenance of personality traits, given the close link between personality and fitness. Though a number of studies have demonstrated potential drivers of interindividual behavioral variation (e.g. life history tradeoffs and heterogeneous selection; Lima 1998; Biro et al. 2004; 2006; Dingemanse et al. 2004; Stamps 2007; Wolf et al. 2007; Quinn et al. 2009), relatively few have examined the role of sexual selection or social effects. Throughout my thesis, there is a strong focus on group phenotypic composition (**Chapters 2 – 5**), and much of my research focuses on the effects of personality on reproductive performance (**Chapters 2 – 4**). An overview of the questions and findings presented in this thesis can be found in Table 1.

Table 1. A summary of the questions examined in this thesis using a dual great tit and red junglefowl study system, the results of the conducted work (green = some evidence, red = no evidence, grey = not tested), and the relevant chapters.

Question	Great Tits	Red Junglefowl	Chapters
Can a focal individual's own personality influence reproductive performance?	No evidence that focal exploration behavior affected extrapair paternity, cuckoldry, proportion of clutch fledged, number of fledglings, or fledgling weight.	In female-biased groups, very fast- and very slow-exploring males mated with more females and suffered lower sperm competition intensity than intermediate-exploring males.	2, 3, & 4
Can the personalities of a focal individual's social and/or potential mates affect its reproductive performance?	No evidence that the exploration behavior of an individual's social mate and/or the group exploration composition of an individual's potential mates affected extrapair paternity, cuckoldry, proportion of clutch fledged, number of fledglings, or fledgling weight.	No evidence that the exploration or boldness of a male's potential mates influenced levels of polyandry.	2, 3, & 4
Can the personality composition of a focal individual's competitors affect its reproductive performance?	No evidence that the group exploration composition of an individual's competitors affected extrapair paternity or cuckoldry.	Faster-exploring males mated with more females when competitors were slower-exploring, on average, and vice versa.	2 & 3
Can aspects of group phenotypic composition, other than group personality composition, modulate the relationship between focal personality and reproductive performance?	As the proportion of blue tits to great tits in an individual's local social environment increased, males with different levels of exploration became more similar in the proportion of their clutch fledged.	Not tested.	4
Can group personality composition affect emergent group properties?	Not tested.	Male and female group exploration and boldness composition predicted the patterns and/or social network structures of sexual harassment, aggressive, and/or affiliative interactions.	5
Can negative frequency dependent sexual selection aid in maintaining personality?	Not tested.	In female-biased groups, the proportion of matings achieved by faster-exploring males grew with increasing proportions of slower-exploring males in a group.	3
Can assortative mating aid in maintaining personality?	No evidence that individuals mated assortatively with respect to exploration behavior.	No evidence that individuals mated assortatively with respect to exploration or boldness. In fact, individuals seemed to mate disassortatively with respect to boldness.	2 & 3
Can heterogeneity the social environment aid in maintaining personality?	Some evidence suggested that heterogeneity in an individual's local species composition may influence selection on exploration behavior. However, by itself, this heterogeneity may not be enough to maintain interindividual variation in exploration behavior.	Not tested.	4

Measuring Personality

Before assessing the effects of personality on social interactions and reproductive performance, methodology must be established for measuring behavioral traits and quantifying interindividual variation and intraindividual consistency in these behavioral traits. While an established protocol was used to measure exploration behavior in great tits in this thesis, I formulated behavioral assays to quantify exploration and boldness in red junglefowl and assess repeatability in these two behavioral traits, finding moderate to high repeatability in both (**Chapter 3**).

When approaching the analyses to calculate the repeatabilities of exploration and boldness in the red junglefowl datasets used in **Chapters 3 and 5**, I ran into the issue of having to calculate repeatability on datasets that were both nonnormally distributed and continuous. Although methods existed to calculate repeatability for gaussian data, count data, proportion data, and binary data prior to this thesis (Nakagawa & Schielzeth 2010), there was no methodology available regarding how to calculate the repeatability of nonnormal, continuous data. Given this, I initiated a collaboration with Professor Shinichi Nakagawa at the University of New South Wales to develop a technique to overcome this hurdle. We decided to use linear mixed models with non-parametric bootstrapping to calculate repeatability estimates and their associated confidence intervals, as such methodology enabled us to discard linear model assumptions (i.e. residual normality), and Professor Nakagawa has written an R script to make this an assessible option for all. This R script will be published alongside the manuscript comprising **Chapter 3 (Appendix 1)**. Researchers have previously dealt with non-normal distributions of continuous personality data by binning data into ordinal or binary groups and calculating repeatability on the simplified dataset (personal communication Jennifer Morinay). The new methodology presented in my thesis will allow future researchers to bypass this step and retain more information in their calculations of repeatability. This will not only benefit scientists working with personality, but it will have general applicability to calculating repeatability.

Effects of focal personality on reproductive performance

There has been extensive work looking at the fitness consequences of a focal individual's personality, with previous studies demonstrating links between personality and survival and between personality and reproduction, across a variety of species (reviewed in Dingemanse & Réale 2005; Smith & Blumstein 2008). In this thesis, I focused on examining the effects of focal exploration behavior in great tits (**Chapters 2 & 4**) and focal exploration and boldness in red junglefowl (**Chapter 3**) on an individual's reproductive performance. Although previous studies have demonstrated that a male's exploration behavior may influence reproductive performance or strategy in the socially monogamous great tit, both in our population and in others (Patrick et al. 2012; Araya-Ajoy et al. 2016; Abbey-Lee et al. 2018), I found no evidence to support this (**Chapters 2 & 4**). I found that neither male nor female exploration behavior predicted extrapair paternity or cuckoldry (**Chapter 2**). Furthermore, I found that the exploration behavior of breeding males and females did not predict a breeding individual's number of fledglings, proportion of clutch fledged, or fledgling weight (**Chapter 4**). In contrast, in the polygynandrous red junglefowl, I found that very fast- and very slow-exploring males mated with more females and suffered lower sperm competition intensity than intermediate-exploring males (**Chapter 3**). These results may be partially explained by males with different exploration types demonstrating different reproductive strategies (e.g. males at both extremes of the exploration spectrum exhibited a lower ratio of waltzes to harassments than intermediate-exploring males). Overall, my results suggest that the personality of a focal individual has the potential to influence reproductive performance and strategy, thus adding to a growing body of literature on this subject.

Effect of the social environment on reproductive performance

Although a large number of studies have focused on how a focal individual's personality influences fitness, far fewer have examined the effects of the social environment. In addition to the reproductive consequences resulting from an individual's own personality, an individual's

reproductive performance may be influenced by the personality of its social mate, as has been found in Wytham great tits (Patrick et al. 2012), or by the personalities of its potential mates. Interestingly, in **Chapter 2**, I found no evidence to suggest that the personality of a great tit male's social mate or the group personality composition of his neighboring potential mates affected the extrapair paternity he gained or the cuckoldry he suffered. I did, however, find that older females were more likely to have a social partner who sired extrapair young. To my best knowledge, this provides the first evidence that the age of a male's social partner predicts his likelihood of extrapair paternity. Similarly, in **Chapter 3**, I did not find evidence that female personality influenced levels of polyandry in red junglefowl, suggesting that female phenotypes did not influence male reproductive performance.

An individual's competitive environment may also affect its reproductive performance. Group phenotypic composition may be defined as any characterization of a group's phenotypic makeup (e.g. mean phenotype, phenotypic variance, or presence or absence of a given phenotype; Pruitt & Ferrari 2011; Pruitt & Riechert 2011), and previous work has suggested that competitor personality composition may affect the fitness of individuals (Pruitt & Ferrari 2011; Pruitt & Riechert 2011; Sih et al. 2014). In **Chapter 3**, I found that competitor exploration composition influenced the relationship between focal male personality and reproductive performance in female-biased red junglefowl groups. Specifically, I found that faster-exploring males mated with more females than slower-exploring males when their competitors were slower-exploring, on average, while slower-exploring males mated with more females when their competitors were faster-exploring, on average. In contrast, in **Chapter 2**, I examined the effects of neighboring competitor personality composition on extrapair paternity and cuckoldry in great tits, and I found no effect of competitor personality composition on either, regardless of the phenotype of the focal male. To the best of my knowledge, all preceding investigations on group personality composition have been conducted on invertebrate systems, and my thesis is the first body of work to examine the effects of group personality composition in a vertebrate system.

In addition to competitor personality composition, it is also possible that other aspects of the group phenotypic composition of an individual's competitive environment might affect relationships between focal personality and reproductive performance (Cote et al. 2008; Quinn et al. 2009; Le Galliard et al. 2015; Nicolaus et al. 2016). Nevertheless, few studies have explored this possibility. In **Chapter 4**, I examined how the ratio of blue tits (*Parus caeruleus*) to great tits in an individual's local social environment (i.e. species composition) affected the relationship between personality and reproductive output, and the relationship between age and reproductive output, in great tits. I found that with increasing ratios of blue tit to great tit neighbors, which should equate to decreasing competitive pressure, males with different personality types converged in the proportion of their clutch fledged. I found a similar interaction with respect to age in that, with increasing ratios of blue tits to great tits, males of different ages became more similar in the proportion of their clutch fledged.

Overall, my results suggest that the relationship between focal personality and reproductive performance can be modulated by 1) the personality composition of a focal individual's competitors and 2) other aspects of the phenotypic composition of a focal individual's competitive environment, in this case, local species composition.

Maintenance of interindividual variation in personality

Though various hypotheses have been put forth to explain why interindividual variation in behavior is maintained, such as life history tradeoffs, heterogenous selection, disruptive selection, negative frequency dependent selection, and assortative mating, few studies have performed empirical tests of each hypothesis (Dall et al. 2004; Schuett et al. 2010; Nicolaus et al. 2016; Pruitt et al. 2019). Thus, little is understood as to why individuals do not converge on a single personality type, if personality is closely tied to fitness. Past work has suggested that environmental heterogeneity might aid in the maintenance of personality traits (Dingemanse et al. 2004; Cote et al. 2008; Quinn et al. 2009; Le Cœur et al. 2015; Le Galliard et al. 2015). Past work has also suggested that life history tradeoffs, such as tradeoffs between current and future reproduction (Wolf et al. 2007) or between

growth and mortality (Lima 1998; Biro et al. 2004; 2006; Stamps 2007) may help maintain interindividual differences in behavior. Furthermore, some evidence of negative frequency dependent selection occurring at the colony level has been presented in the social spider, *Stegodyphus dumicola* (Pruitt et al. 2019). My thesis enhances this growing body of work by providing evidence suggesting potential roles for negative frequency dependent sexual selection and heterogeneous selection in the maintenance of personality.

The finding in **Chapter 3** of my thesis that, the proportion of matings attained by faster-exploring males increased with increasing proportions of slower-exploring males in female-biased red junglefowl groups, suggests that negative frequency dependent sexual selection may be, at least partially, responsible for maintaining exploration, provided that it is a heritable trait. This represents some of the first evidence of a role of negative frequency dependent sexual selection on the maintenance of personality and denotes a major contribution to the field of animal behavior.

I also examined whether assortative mating could explain the maintenance of interindividual variation in exploration behavior in great tits, in **Chapter 2**, and in exploration and boldness in red junglefowl, in **Chapter 3**. Although I did not find that individuals mated assortatively with respect exploration behavior in great tits or with respect to exploration or boldness in red junglefowl, there was a tendency for disassortative mating with respect to boldness in red junglefowl. Such disassortative mating is expected to reduce interindividual variation in boldness rather than maintain it, if boldness is heritable (Schuett et al. 2010). Thus, it is likely that maintenance of interindividual variation in boldness may be fostered by some other selective force, and future work should examine this possibility.

Finally, limited work has demonstrated that heterogeneity in an individual's physical or social environment may maintain interindividual behavioral variation in great tits (Quinn et al. 2009; Nicolaus et al. 2016). In **Chapter 4**, I add to this knowledge by demonstrating that males with different personality types converge in their reproductive performance with increasing ratios of blue tits to great tits in their local social environment. This suggests that heterogeneity in an individual's

social environment may influence selection on exploration behavior, and coupled with other selective forces, this heterogeneity could help maintain variation in exploration behavior.

Group level consequences of personality

While **Chapters 2 - 4** of my thesis focus on individual level consequences of personality, it is important to recognize that if personality influences social interactions within individuals, this will almost certainly have repercussions for the social dynamics of the larger group. Although rare, there is some evidence to suggest that group personality composition can affect emergent group properties (Sih & Watters 2005). In **Chapter 5**, I shift from exploring the effects of group personality composition on the individual, to exploring the effects of group personality composition on the group. I explored whether male and female group personality composition influenced the average number of aggressive, allopreening, and harassment interactions experienced by individuals in groups of red junglefowl. I also employed social network analyses to examine whether group personality composition predicted the network density, network transitivity, and network reciprocity of these interactions, as well as the steepness and linearity of dominance hierarchies. I found that male and female group exploration and boldness composition influenced the mean number, network structure, and/or network transitivity of many of the aforementioned measures, suggesting that the individual phenotypic makeup of a group can indeed influence group level emergent properties. Because social network structure underlies many important processes such as disease transmission and information flow, elucidating predictors of network structure can further our knowledge about these processes. Future work should examine whether group personality composition can promote fitness differences between red junglefowl groups.

General conclusions

Much work has demonstrated a link between personality and sociality, and the information presented in my thesis adds to this existing body of knowledge. This thesis advances our

understanding of how interindividual differences in behavior are maintained, providing some of the first evidence of negative frequency dependent sexual selection on personality, as well as evidence for heterogeneous selection. This thesis also elucidates various intersections between group phenotypic composition and personality, examining 1) the effects of group personality composition on individual fitness and on the relationship between focal personality and reproductive performance, 2) the effects of local species composition on the relationship between focal personality and reproductive output, and 3) the effects of group personality composition on group level dynamics. The work presented in this thesis has the advantage of using a dual study system containing both wild and captive elements. Although this thesis furthers our understanding of the ecology and evolution of animal personality, much work is still needed in this field. In particular, many studies fail to consider how one's social environment affects fitness, choosing only to focus on the effect of an organism's own personality on its success. Future studies should make an effort to consider how the personalities of one's competitors and actual/potential mates might impact fitness measures. Furthermore, surprisingly little empirical work has been conducted to examine how 1) interindividual differences in behavior or 2) intraindividual consistency in behavior are maintained, and large gaps in knowledge remain. Future work should focus on elucidating the mechanisms driving the maintenance of personality, in addition to focusing on its consequences. Ultimately, understanding the causes and consequences of personality may enable us to further our understanding of processes like population and community dynamics, speciation, and response to anthropogenic change.

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