**Personality tests: men are more variable than women, but are males more variable than females?**

***What about:* Sex differences or similarities: are males the more variable sex when it comes to personality?**

**Males and females are not always different: Reassessing greater male variability in animal personalities**

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**Abstract (218 words)**

The idea that men are more variable than women in traits ranging from intelligence to height has been stitched into the fabric of scientific thinking since Darwin. For personality traits, greater variability among men is frequently attributed to biological rather than social factors. This explanation is underpinned by studies in animals reporting that variation in morphology is greater among males than females. There is, however, less evidence for an equivalent sex difference in behaviours that biologists describe as animal personalities. We conducted a large meta-analysis of animal personality studies (2,167 effect sizes from 203 studies of 226 species, categorised into five taxa) to quantify sex differences in means and variances for: boldness, aggression, activity, sociality and exploration. We then tested if greater sexual size dimorphism, indicative of sexual selection, is correlated with sex differences in personality variation, as theory predicts. Overall, sex differences in personality existed in two of 25 taxon-specific tests. Yet there was only a single case of a sex difference in variance, and a single instance where there was a significant relationship between sexual dimorphism and sex differences in personality means. In both cases females were greater than males. Given these findings we suggest that caution is required before assuming that males and females are more or less variable in personality or other shared traits.

**Introduction**

Numerous studies have quantified average differences between men and women in traits ranging from height to behaviour, including intelligence and personality. While these studies at times have been controversial, far less attention has been given to documenting sex differences in the level of variability among individuals (although see Lehre *et al.* 2009). Despite this, sex differences in behavioural variability and its underlying causes have been at the forefront of discussion in various research fields. For example, sex differences in variability in academic performance (Machin & Pekkarinen 2008) or in the classroom (Baye & Monseur 2016; O’Dea *et al.* 2018; Gray *et al.* 2019) are often linked to reported sex differences in variability in intelligence (Arden & Plomin 2006; Johnson *et al.* 2008), creativity (Ju *et al.* 2015; Karwowski *et al.* 2016), aggressiveness (Deary *et al.* 2003), personality (Borkenau *et al.* 2013) and, ultimately, brain structure itself (Wierenga *et al.* 2020). The general conclusion of these studies is that boys or men tend to be more variable than girls or women. This is often referred to as the ‘greater male variability hypothesis’.

Higher variability among men compared to women in behaviour, personality and cognition is predicted to be due to both social and biological differences between the sexes. Many commentators have, however, argued for the primacy of biological differences (Feingold 1992; Miller & Halpern 2014). For example, Steven Pinker noted that: “*Since a male can have more offspring than a female—but also has a greater chance of being childless (the victims of other males who impregnate the available females)—natural selection favours a slightly more conservative and reliable baby-building process for females and a slightly more ambitious and error-prone process for males*” (New Republic 2005). This line of reasoning is often supported by loose reports that there is a trend across the animal kingdom for males to be more variable than females. While it is true that greater male than female variability in animals has been reported for some traits, the strength and generality of the evidence is mixed. The clearest evidence comes from studies showing greater variability in male than female morphology, especially for traits under sexual selection, including sexual ornaments, courtship displays, weaponry and body size (Price *et al.* 1993; Pomiankowski & Moller 1995; Archer & Mehdikhani 2003; Reinhold & Engqvist 2013; Wyman & Rowe 2014). The evidence is, however, weak or absent for behaviours that are shared by both sexes (Tarka *et al.* 2018; Zajitschek *et al.* 2020).

In the last 15 years, evidence has emerged for consistent behavioural differences in animals that are considered akin to variation in human personality. Human personality is often quantified by classifying individuals based on their scores for five components of behaviour (the ‘Big Five’): extraversion, neuroticism, openness, conscientiousness and agreeableness (Costa & McCrae 1992). Like humans, some animal behavioural traits can also be grouped into five axes that somewhat resemble those in humans: activity, aggression, boldness, exploration and sociability (Réale *et al.* 2007). While greater male variability in human personality has been explored and discussed, sex differences in variability in animal personalities could be a useful comparison to find evolutionary explanations for the existence of personalities, and why men are often more variable than women.

We tend to retain our personality traits over time, and as with most other biological traits, these ‘Big Five’ factors are assumed to have differential costs and benefits arising from more extreme values. For wild animals, consistent and predictable (i.e. repeatable) behaviours that do not change over time or context would appear to be maladaptive. As such, variation in animal personality raises evolutionary questions about how it is maintained in the face of natural selection (Smith & Blumstein 2008; Dingemanse & Wolf 2010). The four main, non-mutually-exclusive explanations invoked by biologists are: (a)sexual selection being more intense among males; (b) negative frequency-dependent selection favouring alternative strategies; (c) life-history trade-offs; and (d) developmental or genetic constraints. Each explanation could potentially apply to both human and animal personalities. Crucially, these explanations might partially account for sex differences in the magnitude of variation in personality: specifically why males are more variable than females.

First, sexual selection is usually stronger on males than females (Fromhage & Jennions 2016; Janicke & Morrow 2018). It tends to favour individuals with the most extreme expression of any trait that increases the likelihood of obtaining mates or fertilizing eggs, because success under sexual competition is determined by relative advantage. Competition generates strong directional selection on traits that improve the access of individuals to mates (e.g. weapons, ornaments and coercive behaviours) (Darwin 1871), or of sperm to eggs (Parker 1970). Sexual selection also tends to favour condition-dependent expression of these costly traits because individuals in better condition can incur greater costs (Rowe and Houle 1996). Even minor differences in resource acquisition among individuals due to chance events or small genetic differences in, say, their foraging efficiency therefore translate into differential expression of sexual traits (Rowe and Houle 1996), increasing phenotypic variance among individuals. Stronger sexual selection on males than females is therefore predicted to result in traits that increase reproductive success and which exhibit greater variance among males than either the equivalent traits among females, or than naturally selected traits in either sex (Pomiankowski & Møller 1995). There is some supporting evidence for this claim. A meta-analysis comparing sex differences in phenotypic variance of traits reported significantly higher variation among males than females for reproductive and non-reproductive traits, but the difference in variance was greater for reproduction-related traits (Wyman & Rowe 2014).

Second, negative frequency-dependent selection can maintain variation in traits. These forms of selection might be particularly important for maintaining variation in behavioural traits (Wolf & McNamara 2012). For example, foraging behaviour in *Drosophila melanogaster* larvae has two genetic polymorphs: ‘rover’ (actively explores and forages) and ‘sitter’ (tends to stay in one place to feed). Under low nutrient conditions, both polymorphs have their highest fitness when they are rare in the population, otherwise too many individuals, of either polymorph, increase competition for limited resources (Fitzpatrick *et al.* 2007). Alternative mating tactics are usually associated with a suite of morphological and behavioural traits that differ from those associated with the dominant mating acquisition tactic (e.g. sneakers tend to be smaller and less colourful than males using the dominant mating tactic). Sexual selection that leads to the evolution of alternative mating tactics will therefore tend to generate higher phenotypic variation among males than females.

Third, life history trade-offs may result in some individuals valuing future reproduction more highly due to a greater life expectancy arising from stochastic, environmental factors (e.g. food availability during development) or gene-environment interactions that favour different genes depending on the prevailing local conditions. These trade-offs could favour shifts in behaviour by individuals with greater life expectancy to be, for example, less bold or exploratory (Wolf *et al.* 2007). Sex differences in population variation in personality as a result seem plausible because many sexually selected traits in males increase the risk of death due to injury during fighting (e.g. fatal bouts in common loons: Piper *et al.* 2008), or elevate mortality because sexual advertising imposes high energetic costs (e.g. field cricket calls: Hunt *et al.* 2004) and attracts predators (e.g. male guppy colouration: Gordon *et al.* 2011). This source of variation is further exacerbated if males vary in the costs that sexually selected traits impose depending on the males’ underlying condition.

Four, greater male variability might arise from distinct genetic and developmental pathways resulting from different sex determination mechanisms (James 1973). In some taxa females have two copies of each gene, while males only have one. In mammals, for example, XX/XY sex determination means that females have two X chromosomes and males a single X chromosome. In females the phenotypic effects of genes on the X chromosome are averaged across their expression on both chromosomes. Averaging occurs either through epigenetic inactivation of different regions of maternally and paternally inherited X chromosomes (Amos-Landgraf *et al.* 2006), or through mosaicism whereby a single X chromosome per cell is expressed (Lyon 1961). In contrast, males only have a maternally inherited X chromosome, so that all genes on it are expressed. All else being equal, this should lead to more extreme phenotypes being exhibited by males than females (review: Charlesworth 1996), hence greater variation among males than among females. It should be noted, however, that females are the heterogametic sex in some taxa, including birds (reviewed in Graves & Shetty 2001), butterflies, and some fish and reptiles (Beukeboom & Perrin 2014). If this were a major mechanism driving differences in variability within the sexes then these taxa would exhibit opposite patterns in trait variability, as has been shown for body size (Reinhold & Engqvist 2013).

Based on the four arguments we have outlined, sexual selection is likely to amplify variation in sexually selected behaviours and, as a by-product, any associated behaviours that contribute to an individual’s personality. For example, in the case of selection on fighting behaviour, this implies that aggressiveness is therefore an aspect of personality where males will be more variable than females. Indeed, in humans, variation in two components of personality (agreeableness and neuroticism) where low and high scores, respectively, are linked to aggressive behaviour, show greater variability among men than among women (Budaev 1999, Archer & Mehdikhani 2003). This line of reasoning should apply to all species where there is stronger sexual selection on males, such that sex differences in personality variation will be greater when there is relatively stronger sexual selection on males. This is a key empirical claim that needs to be tested before attributing greater variation in personality among men than among women to sex-specific evolution.

Here we conduct a large-scale meta-analysis of animal personality studies to test the robustness of broad claims that males show greater variability than females. More specifically, we test three key questions using meta-analytic models: 1) do males show greater variability than females in five personality factors; 2) are sex differences in variability consistent for the five components of personality; and finally 3) does sexual selection (estimated using the proxy of sexual size dimorphism, SSD) explain differences in the magnitude of sex differences in variability in personality? In many taxa the strength of sexual selection is often associated with the magnitude of SSD (Reiss 1986; e.g. primates: Cassini 2020; fish: Horne *et al.* 2020). We therefore included SSD as a moderator in our meta-analysis. Additionally, our data encompassed taxa where males are always heterogametic (mammals), always homogametic (birds), or where taxa have a mixture of the two (insects, fish and reptiles/frogs). As such, we also partially tested for an effect of sex chromosomal arrangement on sex differences in variation in personality by testing for a moderating effect of taxa.

**Results**

*Dataset Summary*

Our final dataset comprised 2,167 effect sizes from five broad taxonomic groups: mammals, birds, reptiles/amphibians (both combined), fish and invertebrates. The number of species (n = 10-106), studies (n = 11-61) and effect sizes (n = 95-674) per taxa are shown in Table 1. Boldness was the most well-studied and sociality the least-studied of the five personality types (n=814 and 166 effect sizes, respectively) (Table 2).

*Sex Differences*

Combining all five personality traits, males and females did not differ significantly in their mean personality in any of the five taxa, nor was there a significant sex difference in variability (Table 1 and Supplementary Table S1). The effect size estimates from our meta-analytic intercept models all had high heterogeneity (*I*2Total SMD > 0.70; *I*2Total lnCVR > 0.60), while there was moderate-low heterogeneity for reptiles/amphibians (*I*2Total SMD = 0.45; *I*2Total lnCVR = 0.01) and fish (*I*2Total lnCVR = 0.49). Heterogeneity within mean personality effect sizes mostly came from between-study differences (*I*2StudyID), while phylogenetic relationships and among species differences (*I*2phylo and *I*2species, respectively) explained heterogeneity in variability of effect sizes for mammals, birds and reptiles/amphibians only (see Supplementary Table S1).

The lack of a sex difference in mean and variability in personality could arise if the direction of any difference in sex-specific values varied across the five personality traits. When the traits were analysed separately we found significant sex differences in mean values in only two cases. Females were significantly more sociable in birds (=-0.68, 95% CIs: -1.16, -0.21; *p*=0.005), but less exploratory in reptiles/amphibians (= 0.25, 95% CIs: 0.05, 0.45; *p*=0.02). There were no significant sex differences in mean values for mammals, invertebrates or fish (Table 2, Figures 1 & 2).

There was only a single significant sex difference in variability when traits were analysed separately; females were more variable in their aggressive behaviour in fish (=-0.13, 95% CIs: -0.25, -0.01; *p*=0.04). There were no significant sex differences in variability in invertebrates, birds, mammals or reptiles/amphibians (Table 2, Figures 1 & 2 and Supplementary Table S2).

*Sexual Size Dimorphism and Personality Differences between the Sexes*

Sexual size dimorphism (SSD) explained sex differences in mean personality in only one of the four taxa tested (Supplementary Table S4), but its influence depended on the personality trait (Table 3). There was no effect of SSD in fish, invertebrates or birds. In mammals, the effect of SSD differed significantly for activity and aggression, but not for boldness or exploration. When the sexes were the same size (SSD=0), males were somewhat more active than females (*β* = -0.09, 95% CIs: -1.29, 1.10; *p*=0.88), and were marginally less aggressive than females (*β* = 0.44, 95% CIs: -1.74, 2.62; *p*=0.69). When males were larger than females (SSD>0), females were significantly more active (*β* =-2.16, 95% CIs: -3.99, -0.32; *p*=0.02) and less aggressive (*β =* 1.36, 95% CIs: -0.01, 2.73; *p*=0.05) than males.

There were no significant relationships between SSD and sex-differences in personality trait variability in any of the four taxa (see Table 3 and Supplementary Table S4). When the sexes were the same size, female fish were more variable in their aggressive behaviour than males (*β* = -0.12, 95% CIs: -0.23, 0.00; *p*=0.05), but when males were larger than females there was no difference in the variability of aggressive behaviour between males and females (*β* = -0.13, 95% CIs: -0.81, 0.55; *p*=0.70). There were no sex differences in variability when the sexes were the same size for any other taxonomic group.

*Publication bias*

We found evidence of publication bias for estimates of sex differences in mean or variances for personality traits in only one of 10 tests. The precision of the study predicted the effect size for the sex difference in the mean for invertebrates (*p* = 0.005; Supplementary Table S12).

**Discussion**

Our results provided very little evidence for widespread male-female differences in personality-linked behaviours in animals in any of the five taxa that we examined. This was the case for both sex differences in the mean values of personality traits, and for the level of variation among individuals. A finer-scale analysis did, however, reveal some sex differences when separately investigating each of the five personality types. Although there were male-female differences for certain personality traits in two of the taxonomic groups, there was no consistent pattern. Specifically, females were significantly more social in birds but less exploratory in reptiles/amphibians. There were no detectable sex differences for mammals, invertebrates or fish. Crucially, there was no evidence for greater male than female variability in any taxa for any of the five personality factors. Indeed, the only instance in which there was a significant sex difference revealed greater variability among females (aggression in fish). Finally, the magnitude of SSD, which is a proxy for the strength of sexual selection on males, explained sex differences in mean personality for activity and aggression in mammals only. When males and females were the same size, males were somewhat more active and less aggressive than females, but as males became larger than females, males became significantly less active and more aggressive than females. However, the magnitude of SSD did not explain sex differences in variability for any of the five personality types in any of the four taxa with sufficient data to test for an effect.

Starting with Darwin (1874, p224) it has been repeatedly stated that males vary more in their appearance (i.e. phenotypes) than do females, partly because of the effects of sexual selection. On closer inspection, however, this empirical claim of greater male phenotypic variability has limited formal empirical support. One general finding from a small-scale, cross-species study is that sexually selected traits in male animals show more variation than naturally selected traits (Pomiankowski & Møller 1995). Given that sexual selection is usually stronger on males this implies that they will exhibit greater phenotypic variation than females when pooled across all traits. However, a different cross-species study showed no significant male-female difference in variation for traits broadly associated with reproduction that are expressed in both sexes, including some traits that might be under direct sexual selection. Furthermore, traits not linked to reproduction had only marginally greater variation among males than females (Wyman & Rowe 2014). In another cross-species study, variation in body size was significantly greater in males than females in taxa where males are the heterogametic sex, but the pattern was reversed in taxa where males are the homogametic sex (Reinhold & Engqvist 2013).

These three cross-species studies focussed heavily on morphological traits, but studies of other types of traits have produced similar findings. For example, a meta-analysis looking at behavioural, physiological and life history traits (e.g. time to maturity) that mediate the link between current and future reproductive effort (i.e. ‘pace-of-life’ traits) reported no significant sex difference in the level of variation among individuals (Tarka *et al.* 2018). There were also no significant male-female differences in variation when the data was analysed separately after being partitioned by breeding system, mating system, study environment or trait type (which included the category ‘behaviour’). Recently, another meta-analysis has investigated a vast dataset on sex differences in what is arguably the most heavily studied model laboratory vertebrate species, the house mouse *Mus musculus* (Zajitschek *et al.* 2020). The main finding is clear: across all examined traits there is no sex difference in trait variability. For specific traits types, however, there is a clear bias towards either females being more variable (e.g. immunological traits, eye morphology) or males being more variable (e.g. morphological traits).

Given the available empirical data it seems that the ‘greater male variability hypothesis’ is not supported for morphological and physiological traits in animals. In contrast, in humans and chimpanzees, greater male variability has been shown for a range of morphological and physiological traits including brain structure (Arnold 2004; van der Linden *et al.* 2017; DeCasien *et al.* 2020) and, perhaps more notably, for behavioural traits like personality (Archer & Mehdikhani 2003; Borkenau *et al.* 2013; Karwowski *et al.* 2016), cognitive ability (Halpern & LaMay 2000; Jones *et al.* 2003; Arden & Plomin 2006; Johnson *et al.* 2008, 2009; Roalf *et al.* 2014) and academic achievement (Lehre *et al.* 2009; Baye & Monseur 2016; O’Dea *et al.* 2018). Our current findings are therefore intriguing, because we show using a larger database of 231 species that personality-like behavioural traits are not more variable in males than females across many different species. If anything, the trend is towards greater variation among females (supporting Tarka *et al.* 2018), which has been previously hypothesised to arise, at least in mammals, due to variation from individuals being at different stages of their oestrus cycle (Beery & Zucker 2011). Our findings for animals raises doubts about the extent to which biological explanations can underpin expectations that men have greater trait variation than women.

One of the most widespread biological explanations for greater variation among men than women is attributed to sex chromosomes and the fact that men are XY and women XX. Men therefore only express genes from a single X chromosome, while women, on average, express genes from both chromosomes. The net effect is greater variance in gene expression among men, which should tend to increase the level of phenotypic variation (Reinhold & Engqvist 2013a). In contradiction to this hypothesis, we found no difference between mammals and birds even though males are heterogametic in mammals and homogametic in birds. One explanation is that genes on sex chromosomes do not affect behavioural traits associated with personality differences in animals. In mammals, genes responsible for body size, brain gender and brain characteristics are X-linked and frequently escape X chromosome inactivation processes that silence gene expression, leading to variability (Carruth *et al.* 2002; Skuse 2006; Snell & Turner 2018).

Another major biological explanation for greater variation among men than women in behavioural traits is sexual selection. This is especially relevant for personality as certain traits are considered to elevate the likelihood of reproducing. For example, more extravert and creative personality types in men attract more mating opportunities in some societies (Buss 1995; Nettle 2006; Karwowski *et al.* 2016). Similarly, there is evidence that consistent levels of aggression (i.e. consistent, average levels of aggression) are correlated with success during male-male competition (e.g. killifish: McGhee & Travis 2010; social lizards: McEvoy *et al.* 2013). These behavioural traits are therefore under direct sexual selection. Sexual selection is expected to result in condition-dependent expression of behavioural traits which should increase phenotypic variation (Gross 1996; Rowe and Houle 1996; Wolf *et al.* 2007). Indeed, there is evidence in humans that traits under sexual selection show a greater sex difference in variability than other traits (Archer & Mehdikhani 2003). It is therefore relevant that we found no moderating effect of sexual size dimorphism, which is a standard proxy for the level of sexual selection on males (e.g. Rohner *et al.* 2016), on the sex difference in variation in personality in any of the animal taxa that we examined, including mammals. One explanation for our finding is that, by emphasizing sexual selection on males, we ignore natural selection on females that might lead to comparable directional selection. For example, females generally invest more than males in parental care (Janicke *et al.* 2016), and, in this context, there might therefore be equally strong selection on females as males to be aggressive. Similarly, in group living animals, females often establish social hierarchies where dominance rank is maintained through aggressive interactions (e.g. Campbell 1999; Kappeler 2017). Another possible explanation for our finding of no evidence for greater male variability in personality is that many of the measures of personality made in animals involve behaviours that are uncorrelated with traits under sexual selection, and likely to be under similar natural selection in both sexes. For example, many animal personality traits affect survival, notably anti-predator responses (as an index of boldness) and foraging (as an index of activity or exploration).

Of course, the fact that we found no evidence for the greater male variability hypothesis in animals for personality traits does not preclude biological factors contributing towards greater male variation in a range of behavioural and allied traits in humans (Snell & Turner 2018). Given that phylogeny (*I*2phylo) explained a large proportion of variance in sex-specific differences in personality variability in mammals it would be valuable to conduct a more focussed meta-analysis looking at sex-specific variability in behavioural traits in primates, or even just the Hominidae. Nonetheless, our findings in animals, alongside rather weak evidence for greater male variability in a suite of other traits (Reinhold & Engqvist 2013; Tarka *et al.* 2018; Zajitschek *et al.* 2020), suggests that accepting evolutionary explanations for greater behavioural variability in men than women is premature. Greater attention needs to be paid to the possible role of social factors that might select for a wider range of developmental pathways in boys than girls and result in greater variability in behaviour among men than women (Gray *et al.* 2019).

**Materials and Methods**

*Literature search and data collection – pre-registration link in here somewhere…*

We conducted a systematic search of the literature for empirical studies of animals that quantify personality traits, which were categorised into five types: ‘boldness’, ‘aggression’, ‘activity’, ‘sociality’ and ‘exploration’ (Sih *et al.* 2004; Réale *et al.* 2007). We ran primary and secondary keyword searches using the search strings shown in Supplementary Table S23. In the primary searches we looked for behavioural measures commonly used by those studying animal personality to quantify each of the five personality types, such as ‘hiding time’ as an index of boldness or ‘distance moved’ as an index of exploration (see Sih *et al.* 2004; Réale *et al.* 2007). Our secondary searches were designed to locate studies of ‘personality-like’ behaviours that were alternate measures of activity, aggression, boldness, exploration or sociality. We then conducted additional forward citation searches to include all articles that had cited one of five influential reviews of animal personality: (Dall *et al.* 2004; Sih *et al.* 2004; Réale *et al.* 2007; Schuett *et al.* 2010; Dingemanse & Wolf 2010). In all cases we searched for studies that collected data on both males and females so that the sexes could be compared in data collected by the same researchers from the same population using equivalent methods. In total, we collected 9,698 records from the *ISI Web of Science* and *SCOPUS* databases on 11 December 2018. The PRISMA diagram summarising our search protocol and the number of articles located using each search method is shown in Fig. 3.

After removing duplicates, 3,739 articles were available for title and abstract screening by LMH. Of these, 942 were excluded at the title/abstract screening stage because they were: a) duplicates (*n* = 130), b) non-animal studies (*n* = 256), c) reviews or non-empirical studies (*n* = 516), d) not in English (*n* = 8), or e) inaccessible (*n* = 32). We then carried out a full-text screening of the remaining 2,797 articles. We included articles in the final dataset only if they provided raw means, variances (i.e. standard error or standard deviation) and sample sizes for behavioural measures of personality for both males and females. Raw summary statistics are required to calculate variance-based effect sizes, which also provide greater opportunities to control for sources of non-independence (Nakagawa *et al.* 2015; Noble *et al.* 2017). Consequently, studies that only report principle components or factor loadings were excluded (see Tarka *et al.* 2018). We excluded articles during full-text screening using the following criteria: 1) it was not a personality study (i.e. reported a behaviour that could not be assigned to any of the ‘Big Five’ categories, e.g. ‘social node position’), 2) the study was on domesticated or agricultural animals, 3) the study did not report separate data for males and females (i.e. the study was on hermaphrodites, clones or gynandromorphs; or data from both sexes were combined; or only one sex was measured; or data was only reported for one sex), or 4) data were unsuitable/missing (i.e. raw data was missing, missing sample sizes, sampling error type was not reported, or mean of one sex was zero leading to effect size calculation issues) (see Figure 3 and Supplementary Material). By definition, personality traits are repeatable (Sih *et al*. 2004), but very few of the available studies reported repeatability, or cited previous work that has documented repeatability of the behavioural measure used to quantify personality. We therefore included all behaviours that are commonly described as being indices of animal personality as long as the authors interpreted behaviours as ‘personalities’ (see Sih *et al.* 2004; Réale *et al.* 2007).

In total, we identified 210 eligible articles that provided us with suitable data to calculate effect sizes (Figure 3). We extracted means, measures of variance (standard deviation or standard error) and sample sizes from the text, tables, figures or supplementary data files for both sexes for all relevant behavioural measures of personality traits that were reported by the authors. We used the R package *metaDigitise* (v1.0.0, Pick *et al.* 2019) to extract summary statistics from figures. The location of the data in the original article is provided in our raw data files (see Supplementary Material).

From our final 210 eligible studies, a further n=7 invertebrate studies were removed from analysis because our model sensitivity checks found that effect sizes calculated from scores were significantly different from the rest of the invertebrate dataset (but not for any other taxonomic group, see Supplementary Table S13). As such, we decided to remove these effect sizes, which reduced our final dataset to n=2,167 effect sizes, n=203 studies and n=226 species.

*Data transformations*

Our dataset contained some means, and associated variances, that needed to be transformed to meet distribution assumptions about normality before we could calculate *g* or lnCVR. First, any latency data (e.g. time to resume behaviour) that was right-skewed was log-transformed using the following calculations to obtain means and standard deviations, respectively:

,

*Eq. 1*

*Eq. 2*

Second, some behavioural measures were presented as proportions, which constrains their distribution, so we converted them to the logit scale: mean= log (p/[1-p]); SD= to meet normality assumptions before calculating the relevant effect size. Information on which effect sizes are based on transformed values are provided in our raw data and code supplied in the Supplementary Materials.

*Effect sizes and sampling variances*

To quantify sex differences in means and variances for personality traits we used unbiased standardised effect sizes. First, to quantify the difference between the sexes in the mean value of personality traits we calculated Hedges’ *g* (sample size adjusted standardised mean difference; Hedges & Olkin 1985) as follows:

,

*Eq. 3*

,

*Eq. 4*

*Eq. 5*

Where is the mean of the behavioural measure, is the pooled standard deviation and N and SD are the sample size and standard deviation for males (M) and females (F), respectively. The associated sampling error variance of Hedges’ *g* is:

*Eq. 6*

We used Hedges *g* instead of log response ratios as some behavioural measures were based on ranks or scores. As such, response ratios could not be calculated because score and rank data are not bound to zero (Houle *et al.* 2011; Nakagawa *et al.* 2015). The relevant direction of the effect size varies depending on the focal behavioural measure of personality. For example, boldness is often measured as either ‘latency to flee’ or ‘time to resume a behaviour’ following a simulated predator approach. Here a bolder individual is therefore indicated by a larger or a smaller value respectively. We examined all measurement protocols and, where necessary, reversed the sign of the male-female difference to ensure that the direction of the effect size had a consistent interpretation for each personality trait. Specifically, a positive value of *g* indicates that males are more social, aggressive, exploratory, active or bold.

Second, to quantify a sex difference in the variance in personality traits we used the log coefficient of variation (lnCVR) (Nakagawa *et al.* 2015). In our data set there was a strong, positive relationship between the mean and variance in personality measurements (males: *r* =0.90; females: *r* =0.91). As such, using lnCVR controlled for mean-variance relationships and allowed us to quantify sex differences in variances independent of the (Nakagawa *et al.* 2015; Senior *et al.* 2020). We calculated lnCVR and its associated samping variance () as follows:

,

*Eq. 7*

*Eq. 8*

where CV*M* and CV*F* are *SDM /M* and *SDF /F* , respectively; and . and are the correlation between the logged means and standard deviations of males and females respectively. A positive value of lnCVR indicates that males are variable than females.

*Moderator variables*

We extracted information on factors that differed among studies where we had an *a priori* expectation that they might moderate the magnitude and/or direction of the effect size (Tarka *et al.* 2018a). Specifically, we recorded the taxa (‘invertebrates’, ‘fish’, ‘amphibians’, ‘reptiles’, ‘birds’, ‘mammals’), the age of individuals (‘juvenile’ or ‘adult’), whether the study population was from the lab (captive breed) or the wild, whether the behaviours were measured in the lab or field, and whether the data was collected in an experiment or during natural behaviour of the subject (‘experimental’ or ‘observational’). Most importantly, we generated two moderator variables to quantify the strength of sexual selection. First, we quantified the degree of sexual size dimorphism (SSD), which is often strongly correlated with indicators of the strength of sexual selection (e.g. primates: Cassini 2020; fish: Horne *et al.* 2020). We calculated SSD as the ratio of male to female mean body length, mass or the size of another focal, dimorphic trait (e.g. wing length) using the following index of SSD (Lovich & Gibbons 1992):

*Eq. 9*

Using the SSD index rather than the sex difference in raw means allows for: 1) a single continuous moderator that is zero when the sexes are the same size, and positive when males are larger than females; and 2) comparison of SSD across a wide range of absolute size measures. Larger values of the SSD index are interpreted as species in which there is increasingly stronger sexual selection on males. Where body size measures for males and females were not reported in the research article, we searched *Web of Science*, *Scopus* and *Google Scholar* using the search terms: “species name” AND male AND female AND body size OR length. For birds, we first searched *CRC Handbook of Avian Body Masses* (Dunning Jr 2007) and the online reference database *Birds of the World* (birdsoftheworld.org; accessed via an ANU library subscription in 2019) for body size measures. We then used data from located studies to calculate the SSD index.

Second, we also quantified mating system (“monogamous” or “multiple mating”). Where included studies did not report mating system, we searched *Web of Science*, *Scopus* and *Google Scholar* using the search terms: “species name” AND “mating system”. The location of data collected for SSD index and mating system are provided in the Supplementary Material.

Based on the number of available studies for different levels of the prospective moderators (age, population source, test location, experimental/observational), or the level of subjectivity required to categorise species (mating system), we decided upon completion of data collection that the only moderators we would formally analyse using a null hypothesis framework for their influence on the effect sizes were the SSD index and taxa. The relationships between the other moderators and the effect sizes are presented in Supplementary Tables S7-S11, but these should be treated as strictly exploratory analyses.

*Meta-analyses*

We modelled the effect sizes Hedge’s *g* and lnCVR using multi-level meta-analytic (MLMA) models (intercept only models that consider random effects) and then ran multi-level meta-regression (MLMR) models (including fixed effect moderators) in R (version 3.5.1, R Core Team 2018) using the package *metafor* (version 2.4.0, Viechtbauer 2010). We ran separate models for each of our five taxonomic groups, namely: birds, mammals, fish, invertebrates and reptiles/amphibians (combined due to low sample sizes). Although we were interested in whether sex differences varied across these taxonomic groups, the available sample sizes generally precluded running models with taxa as a moderator and would have resulted in overly complicated interpretation. Furthermore, the diversity of taxa made it challenging to create a full phylogeny that included all taxa to account for evolutionary relationships and non-independence (Noble et al. 2017). Focusing on broad taxonomic groups separately allowed us to construct phylogenies for each group even though relationships were better resolved for some groups compared to others (e.g., mammal and bird phylogenies were better than phylogenies constructed for insects – see below).

We first estimated the overall evidence for a sex difference in the mean and variance across all personality traits using MLMA models (Table 1). This analysis is based on the simple premise that we predict males will show larger trait values for personality traits (with the possible exception of sociality) (Dingemanse & Wolf 2010; Wolf & Weissing 2010), and greater variance for all five traits in accordance with the ‘greater male variability’ hypothesis (Feingold 1992; Schuett *et al.* 2010). More importantly, this analysis provides a baseline that allows us to look for sources of heterogeneity in the data. To account for the non-independence of data we included species identity and study identity as random effects, as there were multiple effect sizes from the same species or study. We also included an observation level random effect to estimate a residual / within study variance. Without this term, within-study effects are assumed to solely result from sampling variance (see Nakagawa *et al.* 2017). To correct for the non-independence of species due to their shared evolutionary history we also included phylogeny as a random effect. Phylogenetic correlation matrices were derived for each taxa either from existing phylogenetic tree databases (e.g. *BirdTree.org* for birds; Jetz *et al.* 2012, 2014) or using *TimeTree.org* (Hinchliff *et al.* 2015). For the bird phylogeny, we used the Ericson tree backbone (Ericson *et al.* 2006) to generate 1,000 trees and then took a sample of 100 trees. We used *ape* and *phytools* packages in R to generate an average tree from these 100 trees, which we then used in our bird taxa models. TimeTree phylogenies were derived by exporting a list of the relevant species from *TimeTree.org*. If a species in our dataset had no phylogenetic representation we substituted the next closest available species (e.g. same genera or family). In all cases, we resolved synonymous taxa across our dataset so that species were correctly categorised and pruned our trees where needed. In the two initial MLMA models for *g* and lnCVR we derived heterogeneity estimates (*I*2; Higgins & Thompson 2002; Nakagawa & Santos 2012). We partitioned heterogeneity arising among species (*I*2species), studies (*I*2study), and due to phylogenetic heritability (*I*2phylo; Hadfield & Nakagawa 2010; Nakagawa & Santos 2012). The total heterogeneity (*I*2Total), is the proportion of the total variance in effect size estimates excluding total sampling variance (see Supplementary Material for calculations).

Next, we fit separate MLMR models for each taxonomic group that included key moderator variables. Our first set of models included personality type as a moderator to provide an estimate of the mean effect size for each of the five personality factors (i.e. ‘activity’, ‘aggression’, ‘boldness’, ‘sociability’, ‘exploration’) (Table 2). We expected that the magnitude of sex-specific differences in mean values and variance would depend on the type of personality trait, because trait types are likely to be correlated with sex roles (e.g. parental care might affect sociability; Schuett *et al.* 2010), life-histories (e.g. sex-biased dispersal is likely to affect exploration and activity; Cote *et al.* 2010), and sexual selection (e.g. the level of male-male competition or female mate choice might affect male levels of aggression and female levels of exploration; Munson *et al.* 2020). We then tested whether the degree of sexual selection, as measured by sexual size-dimorphism (SSD index), moderated effect sizes. We predicted that species with a greater male-bias in SSD would show stronger sex differences in the mean and variance. However, we also expected the strength of its moderating effect to differ among the personality traits. As such, we fit an MLMR model that included personality type, SSD and their interaction. We only fit interaction terms in these models when there were 10 or more species for each personality type. There were too few data, and low heterogeneity, on reptiles/amphibians to run a model that included any interactions (Table 3).

Studies included in our meta-analysis varied greatly in their design and there were a number of additional sources of non-independence within studies (Noble *et al.* 2017). First, multiple personality traits were quantified on the same sets of individuals (e.g. ‘boldness’ and ‘aggression’). Additionally, some studies measured the same individuals multiple times for the same trait (i.e. repeatability), or for the same trait type using a different test (e.g. several measures of boldness). We conducted a series of sensitivity analyses to ascertain the impact that these sources of non-independence had on our final results. We created correlation matrices among effect sizes that shared the same sets of individuals in the sample used to derive effect sizes. Given that we did not know the exact correlation among traits we created three different dependency matrices (**D**; i.e., correlation matrices) that assumed r = 0.3, r = 0.5 and r = 0.8. We refit our models replacing the identity matrix (**I**) that was assumed when estimating the residual error variance with our **D** matrices.

For all models we present meta-analytic mean estimates and 95% confidence intervals (Tables 1-3).

*Publication bias*

It is possible that published studies might disproportionately report certain findings (e.g. greater male variability). To look for publication bias, we first checked for funnel plot asymmetry for both *g* and lnCVR. Studies with large error (e.g. low precision) drive funnel plot asymmetry if there is a true non-zero effect and a bias towards publishing significant results (REF). Visual inspection of funnel plots is misleading, however, as we need to account for additional sources of variation in effect sizes (i.e. moderator variables and random factors) beyond effect size precision. We therefore included precision as a moderator term in our MLMR models to test where it explained some of the variation in the reported effect sizes (Van Aert *et al.* 2019). If precision has a significant influence, this is suggestive of publication bias. Precision was calculated as:

*Eq. 10*

Where is the sampling variance of effect sizes’ Hedge’s *g* (Eq. 3-6) or lnCVR (Eq. 7-8).

**Data availability**

xxx

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Table 1. Multi-level meta-analytic models for each taxonomic group for a sex difference in the mean (SMD) and variability (lnCVR) in personality traits. Positive estimates indicate that the mean or variability in personality is greater for males than females.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Parameters** | **Overall mean** | **95% CI** | **Prediction interval** | ***t* score** | ***p*-value** | ***n* effect sizes** | ***n studies*** | ***n species*** |
| *SMD (Hedge’s g - Mean)* |  |  |  |  |  |  |  |  |
| Mammals | 0.08 | -0.28, 0.45 | -1.10, 1.27 | 0.44 | 0.66 | 674 | 61 | 45 |
| Birds | -0.14 | -0.36, 0.09 | -1.82, 1.57 | -1.17 | 0.24 | 483 | 50 | 106 |
| Reptiles / Amphibians | 0.07 | -0.08, 0.22 | -0.52, 0.67 | 0.94 | 0.35 | 95 | 11 | 10 |
| Fish | -0.04 | -0.35, 0.28 | -1.00, 0.93 | -0.24 | 0.28 | 493 | 44 | 22 |
| Invertebrates | 0.30 | -0.02, 0.62 | -1.89, 2.48 | 1.82 | 0.07 | 422 | 37 | 36 |
|  |  |  |  |  |  |  |  |  |
| *lnCVR (Variance)* |  |  |  |  |  |  |  |  |
| Mammals | 0.07 | -0.20, 0.34 | -0.64, 0.79 | 0.51 | 0.61 | 674 | 61 | 45 |
| Birds | -0.14 | -0.65, 0.37 | -1.94, 1.64 | -0.56 | 0.58 | 483 | 50 | 106 |
| Reptiles / Amphibians | 0.05 | -0.04, 0.14 | -0.06, 0.15 | 1.13 | 0.26 | 95 | 11 | 10 |
| Fish | -0.04 | -0.09, 0.01 | -0.64, 0.56 | -1.44 | 0.15 | 493 | 44 | 22 |
| Invertebrates | 0.00 | -0.13, 0.12 | -0.77, 0.76 | -0.04 | 0.97 | 422 | 37 | 36 |

Table 2. MLMR models for each taxa with personality type as a fixed moderator. Values highlighted in bold indicate a significant difference (< 0.05) between males and females. Positive estimates indicate that the mean and variability are greater for males than females. These models are graphically represented in Figures 1 & 2.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Parameters** | **SMD**  **mean** | **SMD 95%CI** | **SMD**  ***p-value*** | **lnCVR**  **mean** | **lnCVR**  **95%CI** | **lnCVR**  ***p-value*** | **n effect sizes** | **n studies** | **n species** |
| ***Mammals*** | | | | | | |  |  |  |
| Activity | -0.17 | -0.56, 0.23 | 0.40 | 0.10 | -0.20, 0.41 | 0.50 | 84 | 14 | 12 |
| Aggression | 0.10 | -0.27, 0.48 | 0.59 | 0.11 | -0.20, 0.42 | 0.49 | 87 | 16 | 14 |
| Boldness | 0.15 | -0.20, 0.50 | 0.39 | 0.06 | -0.22, 0.34 | 0.67 | 193 | 27 | 27 |
| Exploration | 0.05 | -0.31, 0.41 | 0.79 | 0.04 | -0.25, 0.34 | 0.78 | 213 | 19 | 16 |
| Sociality | 0.09 | -0.29, 0.47 | 0.64 | 0.06 | -0.25, 0.37 | 0.70 | 97 | 12 | 10 |
|  | | | | | | |  |  |  |
| ***Birds*** | | | | | | |  |  |  |
| Activity | -0.14 | -0.43, 0.15 | 0.35 | 0.05 | -0.24, 0.34 | 0.72 | 63 | 14 | 9 |
| Aggression | -0.14 | -0.43, 0.14 | 0.33 | -0.07 | -0.39, 0.25 | 0.68 | 50 | 11 | 10 |
| Boldness | -0.19 | -0.44, 0.06 | 0.13 | -0.005 | -0.23, 0.22 | 0.97 | 261 | 24 | 96 |
| Exploration | 0.09 | -0.18, 0.36 | 0.51 | -0.25 | -0.50, 0.01 | 0.06 | 78 | 16 | 9 |
| **Sociality** | **-0.68** | **-1.16, 0.21** | **0.005** | 0.14 | -0.38, 0.66 | 0.60 | 31 | 3 | 2 |
|  | | | | | | |  |  |  |
| ***Reptiles / Amphibians*** | | | | | | |  |  |  |
| Activity | -0.05 | -0.45, 0.36 | 0.82 | -0.11 | -0.51, 0.29 | 0.60 | 5 | 3 | 3 |
| Aggression | -0.07 | -0.32, 0.19 | 0.60 | 0.33 | -0.05, 0.72 | 0.09 | 30 | 2 | 2 |
| Boldness | 0.08 | -0.15, 0.31 | 0.68 | 0.10 | -0.13, 0.33 | 0.41 | 25 | 4 | 3 |
| **Exploration** | **0.25** | **0.05, 0.45** | **0.02** | -0.10 | -0.35, 0.14 | 0.40 | 32 | 5 | 4 |
| Sociality | -0.05 | -0.60, 0.50 | 0.86 | -0.12 | -0.76, 0.52 | 0.70 | 3 | 2 | 2 |
|  | | | | | | |  |  |  |
| ***Fish*** | | | | | | |  |  |  |
| Activity | -0.16 | -0.65, 0.33 | 0.53 | -0.03 | -0.16, 0.09 | 0.63 | 92 | 9 | 5 |
| **Aggression** | -0.05 | -0.52, 0.42 | 0.53 | **-0.13** | **-0.25, -0.01** | **0.04** | **95** | **17** | **14** |
| Boldness | -0.16 | -0.63, 0.32 | 0.52 | -0.02 | -0.63, 0.59 | 0.59 | 174 | 24 | 13 |
| Exploration | -0.05 | -0.54, 0.44 | 0.84 | -0.03 | -0.16, 0.09 | 0.62 | 103 | 10 | 7 |
| Sociality | -0.40 | -0.91, 0.11 | 0.12 | 0.07 | -0.11, 0.24 | 0.47 | 29 | 7 | 6 |
|  | | | | | | |  |  |  |
| ***Invertebrates*** | | | | | | |  |  |  |
| Activity | 0.33 | -0.04, 0.70 | 0.08 | -0.06 | -0.19, 0.08 | 0.41 | 166 | 18 | 17 |
| Aggression | 0.35 | -0.36, 1.06 | 0.33 | 0.17 | -0.10, 0.43 | 0.22 | 35 | 5 | 6 |
| Boldness | 0.31 | -0.05, 0.67 | 0.09 | -0.04 | -0.16, 0.08 | 0.56 | 161 | 22 | 22 |
| Exploration | 0.00 | -0.44, 0.45 | 0.98 | 0.07 | -0.12, 0.26 | 0.47 | 54 | 7 | 6 |
| Sociality | 0.39 | -0.38, 1.16 | 0.32 | 0.27 | -0.14, 0.68 | 0.20 | 6 | 1 | 1 |

Table 3. MLMR models with personality trait type and SSD moderator terms for each taxonomic group. Estimates highlighted in bold indicate significant differences between males and females. Positive estimates indicate that the mean and variability are greater for males than females. Separate models were run for each trait type with SSD as a moderator, so personality trait estimates show the mean when males and females are the same size. Only interactions with 10 or more species for each personality type were estimated.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Parameters** | **SMD**  **mean** | **SMD 95%CI** | **SMD**  ***p-value*** | **lnCVR**  **mean** | **lnCVR**  **95%CI** | **lnCVR**  ***p-value*** | **n studies** | **n**  **species** | **n effect sizes** |
| ***Mammals*** | | | | | | |  |  |  |
| Activity | 0.44 | -1.74, 2.62 | 0.69 | 0.05 | -0.15, 0.25 | 0.60 | 14 | 12 | 84 |
| **SSD** | **-2.16** | **-3.99, -0.32** | **0.02** | 0.13 | -0.56, 0.81 | 0.72 |  |  |  |
| Aggression | -0.09 | -1.29, 1.10 | 0.88 | 0.09 | -0.21, 0.39 | 0.56 | 15 | 13 | 85 |
| **SSD** | **1.36** | **-0.01, 2.73** | **0.05** | -0.05 | -1.43, 1.33 | 0.94 |  |  |  |
| Boldness | 0.09 | -0.09, 0.27 | 0.34 | 0.07 | -0.03, 0.16 | 0.16 | 26 | 26 | 163 |
| SSD | -0.16 | -0.50, 0.17 | 0.34 | 0.08 | -0.09, 0.25 | 0.35 |  |  |  |
| Exploration | 0.00 | -0.18, 0.18 | 0.99 | -0.06 | -0.36, 0.24 | 0.69 | 19 | 16 | 213 |
| SSD | -0.05 | -0.60, 0.50 | 0.85 | 0.13 | -0.37, 0.64 | 0.61 |  |  |  |
|  | | | | | | |  |  |  |
| ***Birds*** | | | | | | |  |  |  |
| Boldness | -0.75 | -0.87, 0.33 | 0.38 | 0.03 | -0.04, 0.11 | 0.37 | 21 | 78 | 233 |
| SSD | -0.23 | -1.45, 0.98 | 0.70 | 0.11 | -0.16, 0.37 | 0.44 |  |  |  |
|  |  |  |  |  |  |  |  |  |  |
| ***Fish*** |  |  |  |  |  |  |  |  |  |
| **Aggression** | -0.16 | -0.96, 0.63 | 0.68 | **-0.12** | **-0.23, 0.00** | **0.05** | 16 | 13 | 93 |
| SSD | 0.27 | -0.84, 1.37 | 0.63 | -0.13 | -0.81, 0.55 | 0.70 |  |  |  |
| Boldness | 0.06 | -0.23, 0.34 | 0.70 | -0.04 | -0.33, 0.25 | 0.78 | 23 | 12 | 172 |
| SSD | -0.32 | -0.93, 0.29 | 0.30 | 0.10 | -0.31, 0.52 | 0.63 |  |  |  |
|  |  |  |  |  |  |  |  |  |  |
| ***Invertebrates*** |  |  |  |  |  |  |  |  |  |
| Activity | 0.31 | -0.42, 1.04 | 0.41 | -0.04 | -0.25, 0.17 | 0.72 | 18 | 16 | 165 |
| SSD | -0.66 | -2.26, 0.93 | 0.41 | 0.27 | -0.53, 1.07 | 0.50 |  |  |  |
| Boldness | 0.18 | -0.03, 0.38 | 0.10 | -0.04 | -0.16, 0.09 | 0.56 | 22 | 22 | 161 |
| SSD | 0.28 | -0.54, 1.10 | 0.50 | 0.02 | -0.47, 0.51 | 0.95 |  |  |  |



**Figure 1**. Phylogenetic relationships and orchard plots for a) mammals and b) birds. Node colours reflect SSD ratios for each species (no data is grey) and heatmap data shows *n* effect sizes for each personality trait type for each species. Orchard plots show all effect sizes and mean effect size for SMD and lnCVR MLMR models with personality trait as a moderator term. Thin bars are 95% CIs and thick bars are prediction intervals. Circle size reflects effect size precision where bigger circles have greater precision.



**Figure 2.** Phylogenetic relationships and orchard plots for c) reptiles and amphibians (reptilia), d) fish and e) invertebrates. Node colours reflect SSD ratios for each species (no data is grey) and heatmap data shows *n* effect sizes for each personality trait type for each species. Orchard plots show all effect sizes and mean effect size for SMD and lnCVR MLMR models with personality trait as a moderator term. Thin bars are 95% CIs and thick bars are prediction intervals. Circle size reflects effect size precision where bigger circles have greater precision.



**Figure 3.** *PRISMA* diagram showing the process of finding, screening and including/excluding studies for this meta-analysis. See Supplementary Material accompanying this article for keyword searches.