**No meta-analytic support for greater male variability in animal personalities**

**Abstract (150 words max.)**

Human and animal studies alike often report ‘greater male variability’; males have greater representation at the extreme ends of any trait by virtue of their sex chromosomes. Human personalities generally show greater male variability for personalities that attract the opposite sex, yet it is unclear whether animal personalities show similar patterns. We conducted a meta-analysis of animal personality behaviours (*n*=2,248 effect sizes) across five taxonomic groups (*n*=231 species) to look for sex differences in personalities and the influence of sexual selection (degree of sexual size dimorphism) on trait means and variability. Surprisingly, we found that sex differences in personality generally reflected differences in life-histories rather than sexual selection, and sex differences in trait variance favoured greater female, rather than male, variability. We suggest future studies take caution when discussing greater male variability in shared traits.

**Introduction**

Differences between men and women have been the focus … , especially when it comes to intelligence and behaviour. The idea that there are ‘more male geniuses, more male criminals, more male mental defectives’ persists, in spite of a general lack of sex differences in trait means. This ‘greater male variability’ appears to hold true for a range of behavioural, physiological and morphological traits. For example, male-biased sex

That males often have greater variability than females is a trend observed across the animal kingdom. This ‘greater male variability’ hypothesis appears true for a range of behavioural, physiological and morphological traits (Pomiankowski & Møller 1995). In humans, for example, male-biased sex differences in variability have been reported for traits like intelligence (Arden & Plomin 2006; Johnson *et al.* 2008), birth weights and several blood parameters (Lehre *et al.* 2009), creativity (Ju *et al.* 2015; Karwowski *et al.* 2016) and in personality traits related to intrasexual competition (i.e. aggression; Budaev 1999; Archer & Mehdikhani 2003). Yet the mechanisms behind such widespread, sex-biased trait variation remain unclear. Darwin (1871) was the first to suggest that males might be the more variable sex because males are generally the sex under sexual selection. Therefore, traits important for male fitness should have increased variance, compared to the same traits in females or other non-sexually selected traits, in order for sexual selection to operate (Pomiankowski & Møller 1995; Wyman & Rowe 2014). Additionally, sexually-selected traits are often condition-dependent; because they require time and energy to produce and maintain, increased variability thus reflects male quality (Rowe and Houle 1996). Sexual size dimorphism, where one sex is larger than the other,

For example, mammalian males are the larger sex, male-male competition for females. Sexual size dimorphism is costly in terms of a longer development time for sons, as well as energetic requirements for growth and maintenance of a larger body (reference).

* Such as sexual size dimorphism (SSD) (Cotton *et al.* 2004; Bonduriansky 2007)

*Paragraph 2 – sex chromosome hypothesis and sex differences in variability for SHARED TRAITS*

While it is reasonable to expect male sexual traits to have greater variability than non-sexually selected traits, traits shared by both sexes are also frequently expected to show male-biased variability. For example, …

One explanation for the prevalence of male-biased variability is the ‘sex chromosome’ hypothesis (James 1973; other reference?). For mammals, females have two copies of the X chromosome (homogamety), so the effects of any genes found on the X chromosome become averaged out, either through epigenetic inactivation of some regions during development (Amos-Landgraf *et al.* 2006), or through mosaicism where the ratio of genes on either X chromosome are variably expressed (Lyon 1961). Male mammals, however, only have one copy of the X chromosome (heterogamety), so all genes present on their copy of the X chromosome are fully expressed, leading to more extreme phenotypes and, consequently, higher variances for shared traits (i.e. dosage compensation; see review by Charlesworth 1996). However, not all males are heterogametic – male birds have ZZ sex chromosomal arrangement while female birds have ZW, making males the homogametic sex (reviewed in Graves & Shetty 2001). If sex chromosomal arrangement is the mechanism driving sex-biased variability, species with heterogametic females should have greater trait variability than males. Indeed, in a meta-analysis covering a broad range of taxonomic groups, Reinhold & Engqvist (2013) found that for species with heterogametic males, males had greater variability in body size than did females, and in species with heterogametic females, females had greater variability in body size than males.

* Can also talk about sex differences in mean trait expression for traits, including those not related to reproduction

*Paragraph 3 – sex differences in variability for personality – a shared behaviour under sexual selection? (humans and animals)*

Start off talk about trade-offs as the third explanation – using personalities as my examples

In the realm of human personality, our behavioural quirks can be categorised into one of five factors: Extraversion, Neuroticism, Openness, Conscientiousness and Agreeableness (Costa & McCrae 1992). Like most biological traits, these five factors are continuous and there are costs and benefits associated with personalities that fall along the tail-ends of each. For example, … It is also common to hear that men are often overrepresented at the tail-ends of traits like cognition (e.g. more male geniuses, but also more low-IQ men; Deary *et al*. 2003) and aggression (e.g. overrepresentation in the prison system; reference). And we can see greater male variability in personality traits like Extraversion, Openness, Agreeableness and Conscientiousness, with an absence of any sex differences for Neuroticism (Borkenau *et al.* 2013).

* *Trade-offs with personalities (costs and benefits to scoring high or low on each of the five factor traits) in a human context*
* When we look at the benefits of each trait in an evolutionary context, most seem to benefit males (i.e. more partners, better mating success, more attractive to females)
* So it might then be reasonable to assume that males are the more variable sex when it comes to personality…

*Paragraph 4 – why look at sex differences in animal personality?*

To investigate how prevalent male-biased sex differences in variability for shared behavioural traits are across the animal kingdom, we chose to compare animal personality traits. Animal personalities can be broken down into 5 broad factors, similar to the human five-factor model of personality… Additionally, animal personalities, as part of their definition, must be repeatable for an individual over time, making these traits useful for comparing sex differences between males and females. Finally, the tests used to assess personality are often similar enough to enable comparison over many studies…

* behavioural traits, like personality, might benefit male mating success, are personality traits under sexual selection? Would we see one sex having greater variability in personality than the opposite sex?
* Ecologists and psychologists alike have reasoned that personality traits, for males, might confer mating benefits depending on female preferences, frequency-dependence and environmental conditions. For example,
* Need to talk more about personalities- what kinds of behaviours they encompass etc.

*Paragraph 5 – aims and hypotheses (brief) – basically like first paragraph of methods section*

How ubiquitous are sex differences in variability for shared behavioural traits? In humans, for example, traits linked to sexual selection or mating strategies tend to have greater male variability (Archer & Mehdikhani 2003). For animals, sex differences in variability for animal personality traits are reported, but how universal are they? What are the mechanisms underlying such differences in shared behavioural traits?

* Talk about the Tarka paper in here, how we plan to expand on their findings by focusing on personality traits only …
* Because a lot of empirical studies report sex differences in the mean personalities of males and females, we also decided to include and compare the means of males and females. We needed to collect means and their variability in order to calculate our variability effect sizes, so it makes sense to compare means too. Means also provide information about population-level personality traits, which is important to understand too … something like that to make it clearer why we are also looking at the means
* We chose to include SSD as an additional moderator in our meta-analysis because it is a good proxy for the strength of sexual selection (i.e. larger male size reflects a condition-dependent trait, polygynous mating system, and/or different sex roles; Reiss 1986). Additionally, the inclusion of SSD as a moderator should disentangle the expected roles of sexual selection and sex chromosomal arrangement on sex-biased variability. First, we expected that if males do have greater variability than females in their personality traits, because of sexual selection, then SSD would be a significant moderator of such differences. Second, if sex chromosomal arrangement drives sex differences in behaviour, we should see greater male variability in taxonomic groups where males are the homogametic sex (i.e. mammals) and greater female variability in taxonomic groups where females are the homogametic sex (i.e. birds).
* Hypothesis testing for variability:
  1. Greater male variability – males will be more variable than females overall and for each personality trait (aims 1 & 2)
  2. Sex chromosome hypothesis – males will be more variable than females, especially in taxonomic groups with homogametic males – for which SSD is a good proxy (aims 1, 2 & 3)
  3. Sexual selection – males will be more variable than females especially for traits related to male reproduction and for species with male-biased SSD (a good proxy for sexual selection) (aims 2 and 3)
* Hypothesis testing for mean difference:
  1. Males and females might share similar means, like several human personality trait studies, except for personality traits that reflect different sex roles (i.e. female-biased dispersal, territoriality, parental care, mating system)
* We have 3 main aims which we used to form our 3 main meta-analytic models:
  1. Do males and females differ in either their central tendency or variability in personality-like behaviour?
  2. Are there sex differences in mean or variability for the different personality trait types?
  3. Does the degree of sexual size dimorphism explain sex differences in mean or variability?

**Results**

*Summary of Effect Size Dataset*

Our final dataset contained n=2,248 effect sizes across five taxonomic groups: Mammals, Birds, Reptilia (amphibians and reptiles combined), Fish and Invertebrates. Birds were the most diverse group in our meta-analysis (n=107 unique species), while Mammals had effect sizes from more studies (n=61 studies) than any other group (Table 1). Reptilia was the least represented group with n=10 species and n=95 effect sizes. Boldness was the most well-studied personality type and Sociality the least-studied personality type, with n=825 and n=169 effect sizes, respectively (Table 2).

*No Sex Differences in Personality*

Across all traits measured, males and females did not differ in personality for all taxonomic groups (birds: = -0.13, 95% CIs: -0.36, 0.10; fish: = -0.04, 95% CIs: -0.35, 0.28; invertebrates: = 0.24, 95% CIs: -0.03, 0.51; mammals: = 0.08, 95% CIs: -0.28, 0.45; reptiles: =0.07, 95% CIs: -0.52, 0.67). Variability in behavioural traits was similar for males and females across all traits and taxonomic groups (birds: = -0.15, 95% CIs: -0.66, 0.36; fish: = -0.04, 95% CIs: -0.09, 0.01; invertebrates: = -0.02, 95% CIs: -0.09, 0.06; mammals: = 0.07, 95% CIs: -0.20, 0.35; reptiles: =0.05, 95% CIs: -0.04, 0.14) (see Table 1 and Supplementary Table S1).

*‘Big Five’ Personality Axes*

When personality traits were broken down into the Big Five (Activity, Aggression, Boldness, Exploration and Sociality/Sociability) we found significant sex differences in both the means and the variability for some personality traits within some taxonomic groups.

Female birds were more sociable than males (=-0.68, 95% CIs: -1.16, -0.21, *t* = -2.83, *p*=0.005), male invertebrates were more aggressive than females (=0.45, 95% CIs: 0.00, 0.90, *t* = 1.98, *p*=0.05), and were bolder than females (=0.32, 95% CIs: 0.01, 0.62, *t* = 2.04, *p*=0.04), and male reptiles were more explorative than females (= 0.25, 95% CIs: 0.05, 0.45, *t* = 2.44, *p*=0.02). In contrast, there were no significant sex differences in mean personality for any of the Big Five traits for mammals or fish (see Table 2, Figures 1 & 2).

Female birds had greater variability in their exploratory behaviour than did males (=-0.26, 95% CIs: -0.52, 0.00, *t* = -1.97, *p*=0.05), and female fish had greater variability in aggressive behaviour compared to males (=-0.13, 95% CIs: -0.25, -0.01, *t* = -2.10, *p*=0.04). There were no sex differences in variability for any other personality trait for birds and fish, and we found no significant sex differences in the variability of invertebrates, mammals or reptiles for any of the five personality types (see Table 2, Figures 1 & 2 and Supplementary Table S2).

*Degree of Sexual Size Dimorphism Impacts Personality Differences between Sexes*

Sexual size dimorphism (SSD) alone did not significantly moderate sex differences in personality for any taxonomic group (Supplementary Tables S5 & S6), but SSD did interact significantly with some personality traits (Table 3). The degree of sexual size dimorphism between males and females did not significantly influence boldness behaviour in birds (intercept: *β* =-0.25, 95% CIs: -0.85, 0.34, *t* = -0.84, *p*=0.40; SSD: *β* =-0.24, 95% CIs: -1.45, 0.97, *t* = -0.39, *p*=0.70), nor did it significantly moderate aggressive or boldness behaviour in fish (aggression: *β* =-0.09, 95% CIs: -0.66, 0.47, *t* = -0.32, *p*=0.75; boldness: *β* =-0.13, 95% CIs: -0.70, 0.44, *t* = -0.44, *p*=0.66; SSD x aggression: *β* =0.16, 95% CIs: -0.85, 1.17, *t* = 0.31, *p*=0.76; SSD x boldness: *β* =-0.38, 95% CIs: -1.45, 0.69, *t* = -0.70, *p*=0.48)*.* For invertebrates, SSD significantly interacted with boldness; as males became larger than females (SSD became more male-biased) males were much bolder than females (boldness: *β* =0.37, 95% CIs: -0.02, 0.76, *t* = 1.89, *p*=0.06; SSD x boldness: *β* =1.29, 95% CIs: 0.22, 2.36, *t* = 2.37, *p*=0.02). SSD did not interact significantly with activity within invertebrates; as SSD became more male-biased there was a non-significant trend for females to be more active than males (activity: *β* =0.03, 95% CIs: -0.37, 0.42, *t* = 0.13, *p*=0.90; SSD x activity: *β* =-0.87, 95% CIs: -2.15, 0.42, *t* = -1.32, *p*=0.19). Finally, SSD interacted strongly and significantly with all personality traits (except sociality for which there was not enough data) for mammals. As SSD became more male-biased, females were more active than males (SSD x activity: *β* =-2.02, 95% CIs: -2.94, -1.10, *t* = -4.31, *p*<0.0001), but males were more aggressive (SSD x aggression: *β* =3.45, 95% CIs: 2.05, 4.85, *t* = 4.85, *p*<0.0001), were bolder (SSD x boldness: *β* =1.96, 95% CIs: 0.96, 2.96, *t* = 3.86, *p*=0.0001), and more explorative than females (SSD x exploration: *β* =1.92, 95% CIs: 0.91, 2.92, *t* = 3.75, *p=*0.0002). There were non-significant interactions with SSD for all personality trait types for all taxonomic groups for trait variability (see Table 3 and Supplementary Table S4).

*Mating system, age, population, study environment and study type can influence personality*

Monogamous and multiple mating systems were not significantly different from each other for means or variability for any of the taxonomic groups (Supplementary Table S?). Mean personality effect sizes for adults were marginally significantly different to juveniles for invertebrates (intercept: =0.24, 95% CIs: -0.03, 0.51, *t* = 1.74, *p*=0.08; juvenile: =-0.03, 95% CIs: -0.34, 0.28, *t* = -0.18, *p*=0.86), but not any other taxonomic group, and not for variability (Supplementary Table S?). Fish from the wild had greater differences in variability than fish from lab populations (intercept: =-0.09, 95% CIs: -0.18, -0.01, *t* = -2.11, *p*=0.04; lab: =0.08, 95% CIs: -0.02, 0.19, *t* = 1.55, *p*=0.12), but not for mean personality differences (Supplementary Table S?). Studies conducted in the lab were significantly different to field studies for mammals (intercept: =0.24, 95% CIs: -0.09, 0.57, *t* = 1.44, *p*=0.15; lab: = -0.31, 95% CIs: -0.56, -0.05, *t* = -2.34, *p*=0.02), but not for variability, and not for any other taxonomic group (Supplementary Table S?). Finally, effect sizes from observational studies were significantly different from experimental studies for mammals (intercept: =0.00, 95% CIs: -0.21, 0.22, *t* = 0.03, *p*=0.98; observation: = 0.39, 95% CIs: 0.13, 0.64, *t* = 2.39, *p*=0.004), but not for variability, and not for any other taxonomic group (Supplementary Table S?).

*Publication bias*

We found evidence of publication bias for means reported in invertebrate studies, but not for variability, and not for any other taxonomic group (Supplementary Table S?).

**Discussion**

Surprisingly, our meta-analysis failed to find significant sex differences in either trait means or trait variability for personality-like behaviours. When personalities were divided into their respective trait type (the Big Five) we found several significant sex differences in means for some personality types within some taxonomic groups (birds: Sociality; reptilia: Exploration; invertebrates: Aggression, Boldness). However, only exploratory behaviour for birds and aggressive behaviour for fish had significant sex differences in variability, both skewing towards females. Finally, personality and SSD interacted significantly to show strong sex-bias for mean personality, yet only within mammals (male-bias for all personality types except activity, which had a female-bias) and fish (female-biased aggression), and did not moderate sex differences in variability for any personality type or taxonomic group.

Despite suggestions that greater male variability should exist for most shared traits (e.g. Reinhold & Engqvist 2013), the scarcity of male-biased sex differences found by our meta-analysis hints that greater male variability might be true only for traits important for reproduction. First, we found almost no male-bias in either trait means or variability for behavioural types where we expected strong male-bias (e.g. aggression). This result was surprising given that male aggression should correlate with male-male competition and reproduction (reference). In contrast, human antisocial personality types (equivalent to aggression in animals) show greater male than female variability (references). Aggressive personality traits in humans are thought to be maintained by negative frequency-dependant selection whereby it’s beneficial for male reproductive success to have fewer extremely aggressive males in the population (references). Second, our chosen sexual selection moderators (SSD and mating system) did not significantly change either mean trait expression or variability; while SSD did interact with personality trait type for mean trait expression in mammals, SSD had no significant effect on variability for any taxonomic group. As such, it’s unlikely that sexual selection plays a major role in the maintenance of personality-like behaviours in animals.

* So what about human personality? A lot of personality axes with strong male bias are thought to be maintained by negative frequency dependant selection and to be important for reproduction. Other personality traits often have no difference in means or variability between males and females
* Archer and Mehdikhani (2003) talk about and compare means and variances between males and females for personality-like traits related to sexual selection and unrelated to sexual selection. They found that traits related to sexual selection (directly like physical aggression, or indirectly through a change in reproductive strategy) consistently had significant greater male variability, while traits unrelated to sexual selection had no difference in variability, but often greater female means. *Good paper to relate my main finding that, depending on the context under which a personality trait is measured, there’s likely to be no sex differences in variability! Especially where a trait is related to survival…*

For non-sexual shared traits, the sex chromosome hypothesis suggests that trait variability should reflect sex chromosomal arrangement. While we did observe a tendency for mean variability estimates to skew towards the heterogametic sex (especially mammals and birds), most estimates were nonsignificant. Again, this result was surprising considering the number of studies that report underlying sex chromosomal arrangement as the mechanism for greater male trait variability. Greater male than female variability has been reported for traits like personality types in humans (Budaev 1999, Archer & Mehdikhani 2003, Karwowski *et al*. 2016), cognition and intelligence (Halpern & LaMay 2000, Jones *et al.* 2003, Arden & Plomin 2006, Johnson *et al.* 2008, 2009), and for morphological traits like body size (Reinhold & Engqvist 2013), and brain structure (Arnold 2004, Van der Linden *et al*. 2017, DeCasien *et al*. 2020). Importantly, these traits are also considered important for reproduction; in men, extraversion and creative personality types attract more mating opportunities (Buss 1995, Nettle 2006), while body size is a condition-dependent trait important for male-male competition for females (refs). Therefore, we should expect traits related to reproduction to have greater male variability, and not because of sex chromosomal arrangement. Since we did not observe significant sex differences in variability following patterns of sex chromosomal arrangement, animal personalities could encompass behaviours that don’t differentially affect reproductive outcomes for the heterogametic sex. *Garbage*

* Can also mention greater female variability in some traits, like vision (both mice and humans) which might indicate some traits are more beneficial for females to express variation (finding food, seeing predators?) (see Shaqiri *et al*. 2018, and also Suzie’s paper)
* We might see greater male variability in morphological traits, like body size, brain structure and in traits directly related to morphology, like intelligence or cognition (see that chimp paper), but we don’t see such sex differences in behavioural traits ??? This could be explained by behaviours having a complex genetic underpinning (controlled by multiple genes that aren’t sex-linked?) or that personality-like behaviours are important for survival in both sexes so there is no sexual conflict ??? Something like this I guess
* Aggression and invertebrates is probably due to sexual selection, yet we only see differences in mean trait expression and not variability. Females can be aggressive too – reference that female intrasexual aggression paper about the importance of female aggression in parental care, high investment in offspring requires defence… However, inverts might have had a greater mean aggression than females because most female invertebrates, especially the species in our meta-analysis, don’t really provide parental care – although we lacked the parental care data to test this idea.
* Wyman and Rowe (2014) conducted a meta-analysis comparing heritabilities and additive genetic variances of phenotypic traits for males and females. When using a t-test, they found that mean male coefficients of variance were not significantly different from mean female coefficients of variance for non-reproduction-related phenotypic traits, as well as traits important for reproduction. – *this is most similar to my results and more comparable to lnCVR*
  + But there was a significant skew towards male-bias for coefficients of phenotypic variance for reproductive traits, non-reproductive traits, and the entire dataset.
  + Reproduction traits showed more male-biased phenotypic variance than not-reproduction related traits

Personality traits are frequently measured under the context of survival; personality encompasses antipredator responses (‘risky’ behaviour, or Boldness), foraging (Activity/Exploration), and other behaviours related to survival that are important for both sexes. Indeed, we found no sex differences in Activity and only one instance of male-biased Boldness behaviour for invertebrates. Where we did find sex differences in personality, the traits and their direction tended to reflect life-history differences between the sexes. For example, male reptiles were more explorative than females which might indicate male-biased dispersal (e.g. cane toads *Rhinella marina*; reference), while female birds were more sociable than males which likely reflects social group behaviour (e.g. zebra finches *Taeniopygia guttata*; reference). Additionally, because there are costs (e.g. energetic investment) and benefits (e.g. faster growth, more feeding opportunities) associated with the expression of personality types (reference), both sexes likely experience trade-offs that lead to similar trait means and variabilities. Previous meta-analyses have found evidence of trade-offs between personality and survival (Smith & Blumstein 2008, Moiron *et al*. 2020), and we found some evidence that the degree of SSD might impact trade-offs between personality and survival for the sexes differently. For example, strong interactions between SSD and personality trait types for mammals, and between boldness and SSD for invertebrates, show that larger males trade-off risk-adverse behaviour for larger body size. In mammals, as males became larger than females, males became bolder, more explorative and more aggressive than females. Male mammals are quite often the larger sex, due to sexual selection, so as males become larger they likely face more intense male-male competition (reference). Similarly, larger animals are less likely to suffer mortality from predation, but also require more food to fuel their bigger bodies, so males trade-off risky behaviour for increased foraging opportunities.

* Supports pace-of-life I guess

*Where can this bit fit?*

* For our significant measures of phylogeny on heterogeneity (I2) for lnCVR in birds and mammals, we can say that this suggests heritability of personality in these groups – heritability measures the degree of phenotypic variation due to genetic (not environmental) variation. This would suggest that variability in personality traits, for birds and mammals, are not driven by environmental conditions but are instead heritable. As such, any sex differences in variability in personalities would be due to heritable variation
* Greater variability in wild populations? Tarka *et al*. 2018, Smith & Blumstein 2008, Moiron *et al*. 2020

**Materials and Methods**

*Literature search and data collection*

We conducted a systematic review and meta-analysis by systematically searching the literature for empirical studies quantifying animal personality behavioural traits in males and females (as classified by Sih *et al*. 2004 & Réale *et al*. 2007). We collected 9,698 records from both ISI Web of Science and Scopus databases on 11 December 2018, using primary and secondary keyword searches (see PRISMA in Figure 3). A secondary search was used to find and include studies that measured ‘personality-like behaviours’; behaviours not explicitly defined as personalities but were measures of activity, aggression, boldness, exploration or sociality. We also conducted a forwards citation search in both databases to include every record that had cited one of five key animal personality reviews: (Dall *et al.* 2004; Sih *et al.* 2004; Réale *et al.* 2007; Schuett *et al.* 2010; Dingemanse & Wolf 2010).

After removing duplicates, 3,739 records were left for title and abstract screening by LH. A total of 942 papers were excluded at the title/abstract screening stage because they were: 1) duplicates (*n* = 130), 2) non-animal studies (*n* = 256), 3) reviews or non-empirical studies (*n* = 516), 4) were not published in English (*n* = 8), or 5) were inaccessible (*n* = 32). This left 2,797 papers for full-text screening. We included papers in the final dataset only if they provided raw means and some measurement of error for both males and females because raw summary statistics are required for the derivation of variance-based effect size measures and provide greater opportunities to control for sources of non-independence (Nakagawa *et al.* 2015; Noble *et al.* 2017). Studies that only report PCAs and factor loadings were excluded as their interpretation can be challenging (e.g. Tarka *et al*. 2018). Briefly, we excluded papers at the full-text stage if they met the following exclusion criteria: 1) were not personality studies (i.e. studied a behaviour that could not fit into any of the ‘Big Five’ categories, like social node position), 2) studies used domestic or agricultural animals where individuals were neutered, 3) studies did not compare males and females (i.e. studies where animals were hermaphroditic, clonal or gynandromorphs, or where both sexes were analysed together, or only one sex was studied), or 4) data were unsuitable/missing (as shown in Figure 3). By definition personality traits must be repeatable (reference), yet many studies measuring personality did not report repeatability, nor refer to previous studies that have found those traits to be repeatable. We therefore decided to include a broad range of behavioural types that match up with personality studies.

In total, this provided 211 eligible studies with suitable data that could be included in our meta-analysis (see Figure 3). We extracted means, error (standard deviation, standard error) and sample sizes from text, tables, figures and supplementary data files for both males and females on all personality traits described by the study authors. We used the R package *metaDigitise* (v1.0.0, Pick *et al*. 2019) to extract summary statistics from figures where needed.

*Effect size and sampling error*

To understand how males and females differ in their mean personality traits and their variability we used two contrast-based effect size measures. To understand changes in mean personality between the sexes we calculated Hedges’ *g* (sample size adjusted standardised mean difference; Hedges & Olkin 1985) and its associated sampling error as follows:

, *Eq. 1*

*Eq. 2*

Where is the mean, is the pooled standard deviation and N and SD are the sample size and standard deviation for males (M) and females (F), respectively. We used Hedges *g* instead of log response ratios as our chosen effect size as much of the data was not on a ratio scale and as such a response ratio could not be calculated. Effect size direction for a given behavioural trait depended on the way in which it was measured within a study. For example, boldness can often be measured as latency to flee, where a shorter time indicates a shyer individual. Yet the time to resume behaviour following a simulated predator approach, another common boldness measure, means that bolder individuals are those that resume normal behaviour more quickly. As such, we carefully examined all behavioural traits and ensured that the directionality (i.e., larger mean) was always consistent, flipping the direction of effect size estimates to ensure effect size interpretations were consistent.

We had strong mean-variance relationships in our data. As such, to understand differences in variance in personality traits across the sexes we used the log coefficient of variation (lnCVR) (Nakagawa *et al.* 2015), calculating the effect size and samping variance as follows:

,

*Eq. 3*

*Eq. 4*

where CV*M* and CV*F* are *SDM /M* and *SDF /F* , respectively. The lnCVR allows us to quantify the difference in variance between the sexes independent of changes in the mean (Nakagawa *et al.* 2015).

*Data transformations*

Our dataset contained some means, and their variances, that needed to be corrected before we could calculate SMD and lnCVR effect sizes. First, latency data (e.g. time to resume behaviour) that had not been corrected for normality (right-skewed) was log-transformed using the following calculations for means and standard deviations, respectively:

,

*Eq. 5*

*Eq. 6*

Second, proportion data constrain distributions of variances at high and low values, so we converted these data to a logit scale to meet assumptions of normality before calculating effect sizes.

*Moderator variables*

We collected a series of moderator variables that we *a priori* expected to moderate the effect size magnitude and direction. Personality traits extracted for males and females were categorised into one of five types suggested by Réale *et al.* (2007); ‘boldness’, ‘aggression’, ‘activity’, ‘sociality’ and ‘exploration’. We also recorded the taxonomic group (‘invertebrates’, ‘fish’, ‘amphibians’, ‘reptiles’, ‘birds’, ‘mammals’), the age of the sample (‘juveniles’ or ‘adults’), whether the study population was from the lab or the wild, and whether the study was conducted in the lab or field given this is expected to affect behaviour (Tarka *et al*. 2018). We also generated three moderator variables that attempt to capture the strength of sexual selection. First, we quantified the degree of sexual size dimorphism (SSD) between males and females as this is strongly correlated with the strength of sexual selection (e.g. birds: Székely *et al*. 2004; Dale *et al*. 2007; fish: Walker & McCormick 2009; mammals: Promislow 1992). We created an SSD index by taking the ratio of male and female mean body size, mass or another sexually dimorphic trait (e.g. wing length), and used the following calculation (Lovich & Gibbons 1992):

*Eq. 7*

Using a ratio for SSD instead of raw means for male and females allowed us to: 1) have a single continuous moderator for sexual selection that tells us when the sexes are equal in size (0), when males are larger than females (positive values), and when females are larger than males (negative values), and 2) to compare SSD across a range of body size measures and scales. Our second measure attempting to capture the strength of sexual selection was the type of mating system (‘multiple mating’ and ‘monogamous’). Lastly, we also categorised the parental care strategies exhibited by each species within and across studies (‘biparental’, ‘maternal’, ‘paternal’, ‘none’). However, we decided to drop parental care as a moderator term because published data was sparse and unreliable for most species in our dataset. Where body size measures for males and females, mating system and parental care were not reported in the research article itself, we obtained these data by searching Web of Science, Scopus and Google Scholar. We used the search terms: “species name” AND male AND female AND body size OR length (for body size measures), “species name” AND parental care OR mating system for parental care and mating system.

*Meta-analyses*

We modelled SMD (standardised mean difference) and lnCVR (log-coefficient of variance) using multi-level meta-analytic (MLMA) and multi-level meta-regression (MLMR) models in R using the package *metafor* (version ?? Viechtbauer, 2010; R Core Team, 2019). In all our models we subset the data into broad taxonomic groups (i.e., birds, mammals, fish, invertebrates and reptilia (amphibians and reptiles combined due to low sample sizes)) as we were: 1) specifically interested in the extent to which patterns varied across these taxonomic groups and 2) because constructing phylogenies were easier within these sub-groups. We first estimated the overall evidence for a sex-specific effect in mean and variance across all personality traits for each specific taxonomic group using MLMA models. We accounted for effect size measurement error in our model and included study and phylogenetic random effects. We also estimated an observational-level (residual) variance as *metafor* does not estimate this by default. Phylogenetic correlation matrices were derived for each group either from existing phylogenetic tree databases (e.g. BirdTree.org for birds; Jetz *et al.* 2012, 2014) or using TimeTree.org (Hinchcliff, 2015). For the bird phylogeny, we used the Ericson tree backbone (Ericson *et al*. 2006) to generate 1,000 trees and took a sample of 100 trees. We used *ape* and *phytools* in R to take an average tree from these 100 which we used for analyses. TimeTree phylogenies were derived by exporting a list of taxa from TimeTree.org. In some instances, a species that was present in our dataset had no phylogenetic representation so we found and substituted the closest sister species. In all cases, we resolved synonymous taxa across our dataset and trees and pruned our trees where needed. From our MLMA models we derived heterogeneity estimates (*I*2; Thompson & Higgins; Nakagawa & Santos 2012). More specifically we derived between-study heterogeneity estimates (*I*2study), phylogenetic heterogeneity or phylogenetic heritability (*I*2phylo) (Nakagawa & Santos, 2012; Hadfield & Nakagawa, 2010) along with total heterogeneity (*I*2Total), which is simply the proportion of total variance in effect size estimates excluding the total sampling variance.

We also fitted a series of models that included key moderator variables we predicted would explain variation in effect size. In all models, we again controlled for measurement error, study and phylogeny. Our first MLMR model estimated overall-meta-analytic mean estimates for each personality trait type separately (i.e. ‘activity’, ‘aggression’, ‘boldness’, ‘sociability’, ‘exploration’) within each taxonomic group. We expected that any mean and variance differences between the sexes would depend on the type of personality trait measured, especially where trait types are correlated with different sex roles (e.g. parental care; Schuett *et al*. 2010), life-histories (e.g. sex-biased dispersal and exploration or activity trait types; Cote *et al*. 2010), or are under sexual selection (e.g. male aggression might reflect the level of male-male competition or female mate choice; Munson *et al.* 2020). We also tested whether the degree of sexual selection, as measured by 1) the degree of sexual size-dimorphism (SSD) or 2) mating system, moderated effect sizes. We predicted that species with strong SSD or that have multiple mating systems would show stronger differences in mean and variance. However, we also expected such effects to depend on the personality trait being measured. As such, we fitted a model that included personality trait type, SSD and their interaction and a second model that included personality and mating system (we removed the personality trait-level interaction from mating system models due to lack of data). Levels with fewer than 10 species with SSD data were dropped from meta-regression models, and there were not enough data on reptiles to include them in these interaction models (Table 3). We present meta-analytic mean estimates and 95% confidence intervals from our models throughout.

Studies included in our meta-analysis varied greatly in their design and there was 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 identify matrix (**I**) that was assumed when estimating the residual error variance with our **D** matrices.

*Publication bias*

To look for evidence of publication bias in our dataset, we first checked for funnel plot asymmetry across all effect sizes for both SMD and lnCVR. Instead of using an Egger’s regression, we decided to use effect size precision. When studies with small sample sizes (e.g. low precision) are published significantly more often that studies with larger sample sizes, those low-precision studies can drive funnel asymmetry. Therefore, we calculated and included precision as a moderator term in our personality trait MLMR models to look for significance of the slope (Van Aert *et al*. 2019). Where precision was significant, it is likely that publication bias is present. Precision was calculated using the following calculation:

*Eq. 8*

Where is the effect size Hedge’s *g* and its corresponding sampling variance.

**References**

Table 1. Intercept models for each taxonomic group looking for differences in mean (SMD) and variability (lnCVR) between males and females. Positive mean effect sizes reflect a female-bias in mean and variability for personality traits while negative mean effect sizes show male-bias.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Parameters** | **Est. mean** | **95% CI** | **Pred. interval** | ***t score*** | ***p*-value** | ***n* effect sizes** |
| *SMD (Hedge’s g)* |  |  |  |  |  |  |
| Mammals | 0.08 | -0.28, 0.45 | -1.10, 1.27 | 0.46 | 0.65 | 684 |
| Birds | -0.13 | -0.36, 0.10 | -1.85, 1.59 | -1.12 | 0.26 | 493 |
| Reptilia | 0.07 | -0.08, 0.22 | -0.52, 0.67 | 0.94 | 0.35 | 95 |
| Fish | -0.04 | -0.35, 0.28 | -1.00, 0.93 | -0.24 | 0.28 | 493 |
| Invertebrates | 0.24 | -0.03, 0.51 | -1.76, 2.24 | 1.73 | 0.08 | 483 |
| *lnCVR* |  |  |  |  |  |  |
| Mammals | 0.07 | -0.20, 0.35 | -0.64, 0.79 | 0.54 | 0.59 | 684 |
| Birds | -0.15 | -0.66, 0.36 | -1.95, 1.65 | -0.59 | 0.56 | 493 |
| Reptilia | 0.05 | -0.04, 0.14 | -0.06, 0.15 | 1.13 | 0.26 | 95 |
| Fish | -0.04 | -0.09, 0.01 | -0.64, 0.56 | -1.44 | 0.15 | 493 |
| Invertebrates | -0.02 | -0.09, 0.06 | -0.72, 0.69 | -0.44 | 0.66 | 483 |

Table 2. MLMR models with personality trait type for each taxonomic group. Values highlighted in bold indicate significant differences between males and females. Positive mean effect sizes reflect a male-bias in mean and variability for personality traits while negative mean effect sizes show female-bias. 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*** |
| ***Mammals*** | | | | | | |
| Activity | -0.16 | -0.56, 0.23 | 0.41 | 0.11 | -0.19, 0.41 | 0.48 |
| Aggression | 0.11 | -0.27, 0.48 | 0.58 | 0.11 | -0.20, 0.42 | 0.48 |
| Boldness | 0.15 | -0.20, 0.50 | 0.39 | 0.06 | -0.21, 0.34 | 0.65 |
| Exploration | 0.06 | -0.31, 0.42 | 0.77 | 0.05 | -0.24, 0.34 | 0.73 |
| Sociality | 0.09 | -0.29, 0.47 | 0.64 | 0.06 | -0.24, 0.37 | 0.68 |
| ***Birds*** | | | | | | |
| Activity | -0.13 | -0.42, 0.16 | 0.37 | 0.04 | -0.25, 0.33 | 0.79 |
| Aggression | -0.11 | -0.40, 0.18 | 0.47 | -0.06 | -0.39, 0.27 | 0.72 |
| Boldness | -0.19 | -0.44, 0.07 | 0.15 | -0.01 | -0.23, 0.21 | 0.93 |
| **Exploration** | 0.08 | -0.19, 0.35 | 0.56 | **-0.26** | **-0.52, 0.00** | **0.05** |
| **Sociality** | **-0.68** | **-1.16, 0.21** | **0.005** | 0.13 | -1.59, 1.86 | 0.61 |
| ***Reptilia*** | | | | | | |
| Activity | -0.05 | -0.45, 0.36 | 0.82 | -0.11 | -0.51, 0.29 | 0.60 |
| Aggression | -0.07 | -0.32, 0.19 | 0.60 | 0.33 | -0.05, 0.72 | 0.09 |
| Boldness | 0.08 | -0.15, 0.31 | 0.68 | 0.10 | -0.13, 0.33 | 0.41 |
| **Exploration** | **0.25** | **0.05, 0.45** | **0.02** | -0.10 | -0.35, 0.14 | 0.40 |
| Sociality | -0.05 | -0.60, 0.50 | 0.86 | -0.12 | -0.76, 0.52 | 0.70 |
| ***Fish*** | | | | | | |
| Activity | -0.16 | -0.65, 0.33 | 0.53 | -0.03 | -0.16, 0.09 | 0.63 |
| **Aggression** | -0.05 | -0.52, 0.42 | 0.53 | **-0.13** | **-0.25, -0.01** | **0.04** |
| Boldness | -0.16 | -0.63, 0.32 | 0.52 | -0.02 | -0.63, 0.59 | 0.59 |
| Exploration | -0.05 | -0.54, 0.44 | 0.84 | -0.03 | -0.16, 0.09 | 0.62 |
| Sociality | -0.40 | -0.91, 0.11 | 0.12 | 0.07 | -0.11, 0.24 | 0.47 |
| ***Invertebrates*** | | | | | | |
| Activity | 0.08 | -0.23, 0.39 | 0.62 | -0.06 | -0.17, 0.05 | 0.26 |
| **Aggression** | **0.45** | **0.00, 0.90** | **0.05** | 0.02 | -0.17, 0.21 | 0.83 |
| **Boldness** | **0.32** | **0.01, 0.62** | **0.04** | -0.02 | -0.12, 0.08 | 0.65 |
| Exploration | 0.06 | -0.31, 0.43 | 0.74 | 0.05 | -0.10, 0.20 | 0.51 |
| Sociality | 0.30 | -0.26, 0.86 | 0.29 | 0.23 | -0.08, 0.54 | 0.15 |

Table 3. MLMR models with personality trait type and SSD moderator terms, as well as their interactions, for each taxonomic group. Note that some levels were dropped from these meta-regression models due to low sample sizes (fewer than 10 different species with SSD data within each personality trait type). Values highlighted in bold indicate significant differences between males and females.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **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** | **0.27** | **-0.01, 0.54** | **0.05** | 0.07 | -0.22, 0.37 | 0.63 | 14 | 12 | 84 |
| Aggression | 0.15 | -0.06, 0.37 | 0.17 | 0.10 | -0.18, 0.39 | 0.48 | 15 | 13 | 85 |
| Boldness | 0.13 | -0.07, 0.33 | 0.20 | 0.10 | -0.18, 0.39 | 0.48 | 26 | 26 | 163 |
| Exploration | 0.03 | -0.15, 0.22 | 0.72 | 0.04 | -0.24, 0.32 | 0.78 | 19 | 16 | 223 |
| **SSD** | **-2.02** | **-2.94, -1.10** | **<0.0001** | 0.30 | -0.34, 0.94 | 0.36 |  |  |  |
| **Aggression x SSD** | **3.45** | **2.05, 4.85** | **<0.0001** | -0.15 | -1.14, 0.83 | 0.76 |  |  |  |
| **Boldness x SSD** | **1.96** | **0.96, 2.96** | **0.0001** | -0.30 | -1.02, 0.41 | 0.41 |  |  |  |
| **Exploration x SSD** | **1.92** | **0.91, 2.92** | **0.0002** | -0.07 | -0.80, 0.65 | 0.84 |  |  |  |
| ***Birds*** | | | | | | |  |  |  |
| Intercept (Boldness) | -0.25 | -0.85, 0.34 | 0.40 | 0.03 | -0.04, 0.11 | 0.38 | 21 | 78 | 235 |
| SSD | -0.24 | -1.45, 0.97 | 0.70 | 0.10 | -0.16, 0.37 | 0.44 |  |  |  |
| ***Fish*** |  |  |  |  |  |  |  |  |  |
| Aggression | -0.09 | -0.66, 0.47 | 0.75 | -0.11 | -0.31, 0.09 | 0.27 | 16 | 13 | 93 |
| Boldness | -0.13 | -0.70, 0.44 | 0.66 | -0.03 | -0.22, 0.16 | 0.74 | 23 | 12 | 172 |
| SSD | 0.16 | -0.85, 1.17 | 0.76 | -0.28 | -1.03, 0.48 | 0.47 |  |  |  |
| Boldness x SSD | -0.38 | -1.45, 0.69 | 0.48 | 0.39 | -0.44, 1.21 | 0.36 |  |  |  |
| ***Invertebrates*** |  |  |  |  |  |  |  |  |  |
| Activity | 0.03 | -0.37, 0.42 | 0.90 | -0.08 | -0.22, 0.06 | 0.28 | 22 | 19 | 204 |
| **Boldness** | **0.37** | **-0.02, 0.76** | **0.06** | -0.02 | -0.15, 0.11 | 0.79 | 27 | 26 | 178 |
| SSD | -0.87 | -2.15, 0.42 | 0.19 | 0.05 | -0.56, 0.66 | 0.87 |  |  |  |
| **Boldness x SSD** | **1.29** | **0.22, 2.36** | **0.02** | 0.07 | -0.62, 0.76 | 0.84 |  |  |  |



**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 predicted intervals. Circle size reflects effect size precision where bigger circles have greater precision.



**Figure 2.** Phylogenetic relationships and orchard plots for c) 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 (k) 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.



**Figure 3.** *PRISMA* diagram showing the process of finding, screening and including/excluding studies for this meta-analysis. Searches were further refined to agriculture & biology (Scopus), zoology, ecology, biology, multidisciplinary sciences, evolutionary biology (WoS) categories.