

Males are not the more variable sex when it comes to personality

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Abstract

The notion that men are more variable than women is embedded in scientific thinking. For personality traits, this greater variability is partly attributed to biology, underpinned by greater morphological variation among male than female animals. There is, however, little information for animals about sex differences in personality-like behaviours. In a meta-analysis we quantified sex differences in means and variances for five traits: boldness, aggression, activity, sociality and exploration (2167 effects, 203 studies, 226 species). We also tested if sexual size dimorphism, a proxy for sexual selection, explains sex differences. In 25 taxon-trait specific tests we show only two significant sex differences in mean personality, and none for variance. Including size dimorphism explains sex differences in mean personality in two taxon-trait specific tests (aggression, activity in mammals), and in one test for variance (aggression in fish). We find little evidence for widespread sex differences in variability in animal personality.

Introduction

Numerous studies have quantified average differences between men and women in traits ranging from height and physiology to, more controversially, behaviours, including intelligence and personality. Far fewer studies have investigated sex differences in humans in variability among individuals (but see¹). The causes and consequences of sex differences in behavioural variability have, however, been widely debated in the social sciences². For example, sex differences in variability in academic performance³ or the classroom⁴⁻⁶ have been linked to sex differences in variability in intelligence^{7,8}, creativity⁹, aggressiveness¹⁰, personality¹¹ and, ultimately, brain structure¹². The general conclusion is that males are more behaviourally variable than females ('greater male variability hypothesis'), which is sometimes used to explain a male-bias in STEM¹³.

Greater variability among men than women in behaviour, personality and cognition is widely attributed to socio-cultural factors that differ between the sexes, but also to biological factors^{14,15}. Some commentators have, however, argued that the role of biology is underplayed². A key line of reasoning invokes a trend across animals for greater male variability. Although greater male variability has been reported for some traits, the robustness of this claim is unclear. Specifically, the strongest evidence is for greater variability in male than female morphology, especially for sexually selected traits, including ornaments, weaponry and body size¹⁶⁻¹⁸. To date, the evidence is weak or absent for greater male variability for behaviours exhibited by both sexes^{19,20}.

Human personality is often quantified by scoring five components of behaviour (the 'Big Five': extraversion, neuroticism, openness, conscientiousness and agreeableness²¹), which are

repeatability among individuals over time. In the last 15 years, comparable evidence has emerged for behavioural variation among animals that is akin to human personality. These animal behaviours are often grouped into five personality factors that loosely resemble those in humans: activity, aggression, boldness, exploration and sociability²². We can therefore now test claims for greater male variability in personality traits in animals.

Sexual selection on males and sex determination mechanisms are invoked by biologists to explain the maintenance of variation in animal personality^{23,24}, and as evolutionary explanations for sex differences in variability in humans. First, sexual selection is usually stronger on males²⁵. It favours individuals with greater expression of traits that increases the likelihood of obtaining mates (e.g. weapons, ornaments and coercive behaviours²⁶), or fertilising eggs²⁷. Reproductive success depends upon relative competitive advantage. Sexual competition generates strong directional selection and can increase variability in male mating behaviours by promoting the evolution of alternative mating tactics. Sexual selection also favours condition-dependent trait expression because individuals in better condition can incur greater costs²⁸. Even minor differences in resource acquisition among individuals due to chance or small genetic differences in, say, foraging efficiency therefore translate into differential expression of sexual traits²⁸, increasing phenotypic variance among individuals. Stronger sexual selection on males is predicted to yield sexual traits with greater variance among males than equivalent traits in females, or naturally selected traits in either sex^{16,18}.

Sexual selection is likely to amplify variation in sexually selected behaviours and, as a by-product, any associated behaviours that affect personality. For example, sexual selection on fighting behaviour implies that aggressiveness is a personality trait where males will be more variable than females. Indeed, variation in two components of personality

(agreeableness and neuroticism) that are linked to aggressiveness, show greater variability among men^{29,30}. This line of reasoning should apply to all species: male variability in personality should be higher when sexual selection on males is more intense. This prediction is directly relevant to biological explanations for sex differences in variation in human behaviour, but remains untested.

Second, greater male variability might arise from sex determination mechanisms³¹. In mammals, for example, XX/XY sex determination means that females have two X chromosomes and males only one. Therefore in mammalian females the phenotypic effects of genes on the X chromosome are averaged across their expression on both chromosomes, often via epigenetic inactivation of one chromosome³². In contrast, males only express genes on the single, maternally inherited X chromosome. All else being equal, this should create more extreme phenotypes in males³³, hence greater variation among males than females. However, females are the heterogametic sex in some taxa, including birds, butterflies, and some fish and reptiles³⁴. If sex determination drives sex differences in variability then taxa with heterogametic females should exhibit greater variability in females¹⁷.

Here we conduct a large-scale meta-analysis of animal personality studies to test the robustness of claims that males are more behaviourally variable than females. More specifically, we answer three questions: 1) Do males show greater variability than females in five personality factors? 2) Do sex differences in variability differ for the five components of personality? And 3) does sexual selection (estimated using the proxy of sexual size dimorphism, SSD) explain differences in the magnitude of sex differences in the mean and variance in personality? In many taxa, the strength of sexual selection on males is correlated with the magnitude of SSD³⁵. We therefore included SSD as a moderator in our meta-

analyses. Additionally, our dataset contains taxa where males are heterogametic (mammals), homogametic (birds), or a mixture of both (insects, fish and reptiles/frogs). We can partially test if sex chromosomes affect sex differences in variation in personality by testing for a moderating effect of taxa.

We find little evidence for widespread, consistent male-female differences in personality in animals, either for mean values or levels of variation. Crucially, there is no evidence for greater male variability in any taxa for any of the five personality factors. Indeed, the only significant sex difference reveals greater variability among females for aggression in fishes. Finally, the magnitude of SSD, our proxy for sexual selection, only explained sex differences in mean personality for activity and aggression in mammals, but not for variability in any of the taxa-personality types combinations we tested. Our findings for animals, alongside rather weak evidence for greater male variability in animals for other traits, suggests that accepting evolutionary explanations for greater behavioural variability in men than women is premature.

Results

Dataset Summary

Our final dataset comprised 2,167 effect sizes from five broad taxonomic groups: mammals, birds, fish, invertebrates, and reptiles/amphibians (combined). 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 basic meta-analytic intercept models all had high heterogeneity ($I^2_{\text{Total}} \text{SMD} > 0.70$; $I^2_{\text{Total}} \ln\text{CVR} > 0.60$), while there was moderate-low heterogeneity for reptiles/amphibians ($I^2_{\text{Total}} \text{SMD} = 0.45$; $I^2_{\text{Total}} \ln\text{CVR} = 0.01$) and fish ($I^2_{\text{Total}} \ln\text{CVR} = 0.49$). Heterogeneity in the sex difference in mean personality mostly came from between-study differences (I^2_{StudyID}), while phylogenetic relationships and among species differences (I^2_{phylo} and I^2_{species} , respectively) explained heterogeneity in the 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 ($\bar{X}_{\text{SMD}} = -0.68$, 95% CIs: -1.16, -0.21; $p = 0.005$), but less exploratory in reptiles/amphibians ($\bar{X}_{\text{SMD}} = 0.25$, 95% CIs: 0.05, 0.45; $p = 0.02$). While the magnitude of the estimated effect sizes suggest that sex-differences might exist for personality traits in other taxa (e.g., invertebrates and fish) none of the other 23 tests for sex differences in mean personality were statistically significant (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

($\bar{X}_{lnCVR} = -0.13$, 95% CIs: -0.25, -0.01; $p=0.04$). Again, while the magnitude of the estimated effect sizes in other groups were equivalent or even larger for the difference in variance between males and females, none of the 24 other tests were statistically significant (Table 2, Figures 1 & 2 and Supplementary Table S2).

Sexual Size Dimorphism and Sex Differences in Personality

Sexual size dimorphism (SSD) explained the extent of the sex differences in mean personality in only one of the four taxa tested, but its influence depended on the personality trait (Table 3 and Supplementary Tables S5-8). There was no effect of SSD in fish, invertebrates or birds. In mammals, the SSD of a species predicted sex differences in activity and aggression, but not of boldness or exploration. When the sexes were the same size (SSD=0), there were no differences in aggression between males and females ($\beta = -0.09$, 95% CIs: -1.29, 1.10; $p=0.88$). However, as sexual size dimorphism became more male-biased (SSD>0) males were significantly more aggressive than females ($\beta=1.36$, 95% CIs: -0.01, 2.73; $p=0.05$). And when the sexes were the same size (SSD=0) males were no more active than females ($\beta = 0.44$, 95% CIs: -1.74, 2.62; $p=0.69$), but as sexual size dimorphism increased (SSD>0) females were significantly more active than males ($\beta=-2.16$, 95% CIs: -3.99, -0.32; $p=0.02$).

There were no significant relationships between SSD and sex differences in personality trait variability in any of the four taxa in which we could carry out this test (see Table 3 and Supplementary Tables S5-8). When the sexes were the same size, female fish were more variable in their aggressive behaviour than males, but this effect was weak ($\beta = -0.12$, 95% CIs: -0.23, 0.00; $p=0.05$). There were no sex differences in variability when the

sexes were the same size for any other taxonomic group, nor any effect of SSD on the sex difference in variability.

Publication Bias

Overall, we found little evidence that publication bias affected estimates of sex differences in the mean or variance in personality traits. Out of 10 tests, publication bias was only evident for mean personality in invertebrates ($p = 0.005$). After accounting for this, males were, on average, bolder and more active than females (Supplementary Table S14).

Discussion

Starting with Darwin²⁶, 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 this empirical claim of greater male phenotypic variability has limited 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 traits¹⁶. 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, another 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 females¹⁸. 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 sex¹⁷.

These three cross-species studies mainly focussed on morphological traits, but studies of other types of traits have produced similar findings. For example, a meta-analysis of 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 individuals²⁰. There were also no significant male-female differences in variation when the data was 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 probably the most heavily studied model laboratory vertebrate species, the house mouse *Mus musculus*¹⁹. The main finding is clear: across all examined traits there is no sex difference in trait variability. For specific traits types there is, however, a clear bias towards either females (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, at best, only weakly 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^{36,37} and, perhaps more notably, for behavioural traits like personality^{11,30,38}, cognitive ability^{7,8,39,40} and academic achievement^{1,4,6}. Our current findings are therefore intriguing, because we show using a larger database of 226 species that personality-like behavioural traits are, in general, not more variable in males than females. If anything, the trend is towards greater variation

among females (supporting previous work²⁰), which has been hypothesised to arise, at least in mammals, due to the effect of females being at different stages of their oestrus cycle¹⁹. Our findings for animals raises doubts about the extent to which biological factors and evolutionary arguments explain why men have greater trait variation than women for behavioural traits.

One widespread biological explanation 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 on both. The net effect is greater variance in gene expression among men, which should tend to increase the level of phenotypic variation¹⁷. However, we found no difference in the sex difference in variability 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, or only weakly affect, behaviours associated with personality in animals. In comparison, for mammals at least, genes responsible for both cognitive ability and brain structure are thought to be X-linked⁴¹, which might partially explain the strength of sex differences in variability found for both traits.

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 elevate the likelihood of reproducing. For example, more extraverted men tend to have more mating opportunities in some societies⁴². Similarly, there is evidence that consistent, average levels of aggression elevate success during male-male competition⁴³. These behavioural traits are therefore sexually selected. Sexual selection is expected to result in condition-dependent expression of traits which should increase phenotypic variation^{28,44}.

Indeed, there is evidence in humans that some traits under sexual selection show a greater sex difference in variability than other traits³⁰. 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 males⁴⁵, 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 natural selection on females might lead to comparable directional selection. For example, females generally invest more than males in parental care⁴⁶, 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 is maintained through aggressive interactions⁴⁷. Additionally, we might find greater female variability, especially in traits like aggression or sociability, when measurements of personality assays overlap with reproductive periods. Another possible explanation for not finding greater male variability in personality in animals is that many of the measures of personality involve behaviours that are likely to be under similar natural selection in both sexes. For example, many animal personality traits affect survival, notably boldness, which is linked to anti-predator responses, and activity or exploration, which is linked to foraging.

Of course, a lack of evidence for greater male variability in animals for personality traits does not preclude biological factors contributing towards greater male variation in a range of behavioural and allied traits in humans⁴⁸. Given that phylogeny (I^2_{phylo}) 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 behaviour in primates. Nonetheless, our findings for animals, alongside the weak evidence for greater male variability in other traits^{17,19,20}, suggests that accepting evolutionary explanations for greater behavioural variability in men than women is

273 premature. Greater attention needs to be paid to the possible role of social factors that might
274 select for a wider range of developmental pathways in boys than girls yielding greater
275 behavioural variability in men than women⁵.

Materials and Methods

Literature search and data collection

This meta-analysis was pre-registered with the Open Science Foundation (OSF; study details available at: <https://osf.io/bwjyt/>). 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’^{22,49}. We ran primary and secondary keyword searches using the search strings shown in Supplementary Table S25. 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^{22,49}. 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 any of five influential reviews of animal personality^{22,24,49–51}. In all cases we searched for studies that collected data on both males and females so that the sexes could be compared for 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 Figure 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 sexes. Raw summary statistics are required to calculate variance-based effect sizes, which also provide greater opportunities to control for sources of non-independence^{52,53}. Consequently, studies that only report principle components or factor loadings were excluded (e.g.²⁰). 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) (Figure 3 and Supplementary Material). Recently, there has been a push for stricter definitions of personalities in animal behaviour studies⁵⁴. By definition, personality traits are repeatable⁴⁹, 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. As such, many earlier studies of personality-like animal behaviours do not necessarily meet these criteria. To ensure sufficient sample sizes, we therefore included behaviours that are commonly described as indices of animal personality, and also where the authors interpreted behaviours as ‘personalities’^{22,49}.

In total, we identified 210 eligible articles 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* version 1.0.0⁵⁵ 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 S15). 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 had to be transformed to meet distribution assumptions about normality before we could calculate g or $\ln\text{CVR}$. 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:

$$\ln\bar{X} = \log(\bar{X}) - \log\sqrt{1 + \left(\frac{SD^2}{\bar{X}^2}\right)},$$

Eq. 1

$$\ln SD = \sqrt{\log\left(1 + \left(\frac{SD^2}{\bar{X}^2}\right)\right)}$$

Eq. 2

Second, some behavioural measures were presented as proportions, which constrains their distribution, so we converted them to the logit scale: $\text{mean} = \log(p/[1-p])$; $SD = \sqrt{(SD^2) * (1/p) + (1/(1-p^2))}$ 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 difference⁵⁶) as follows:

$$g = \frac{\bar{X}_M - \bar{X}_F}{SD_p} J,$$

Eq. 3

$$SD_p = \sqrt{\frac{(N_M - 1)SD_M^2 + (N_F - 1)SD_F^2}{N_M + N_F - 2}},$$

Eq. 4

$$J = 1 - \frac{3}{4(N_M + N_F - 2) - 1}$$

Eq. 5

Where \bar{X} is the mean of the behavioural measure, SD_p 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:

$$V_g = \left(\frac{N_M + N_F}{N_M N_F} + \frac{d^2}{2(N_M + N_F)} \right) J^2$$

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^{52,57}. 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)⁵². 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 mean^{52,58}. We calculated lnCVR and its associated sampling variance (s_{lnCVR}^2) as:

$$\ln\text{CVR} = \ln\left(\frac{CV_M}{CV_F}\right) + \frac{1}{2(N_M-1)} - \frac{1}{2(N_F-1)},$$

Eq. 7

$$s_{lnCVR}^2 = \frac{SD_M^2}{N_M \bar{X}_M^2} + \frac{1}{2(N_M-1)} - 2\rho_{\ln \bar{X}_M, SD_M} \sqrt{\frac{SD_M^2}{N_M \bar{X}_M^2} \frac{1}{2(N_M-1)}} + \frac{SD_F^2}{N_F \bar{X}_F^2} + \frac{1}{2(N_F-1)} - 2\rho_{\ln \bar{X}_F, SD_F} \sqrt{\frac{SD_F^2}{N_F \bar{X}_F^2} \frac{1}{2(N_F-1)}}$$

Eq. 8

where CV_M and CV_F are SD_M/\bar{X}_M and SD_F/\bar{X}_F , respectively; and $\rho_{\ln\bar{X}_M, \overline{SD}_M^2}$ and $\rho_{\ln\bar{X}_F, \overline{SD}_F^2}$ are the correlation between the logged means and standard deviations of males and females respectively. A positive value of $\ln\text{CVR}$ 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 size²⁰. 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 selection³⁵. 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 SSD⁵⁹:

$$SSD \text{ index} = \left(\frac{\bar{X}_{M_{bodysize}}}{\bar{X}_{F_{bodysize}}} \right) - 1$$

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*⁶⁰ 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 S9-S13, 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 3.5.1⁶¹ using the package *metafor* (version 2.4.0)⁶². 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 an 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-independence⁵³. Focusing on broad taxonomic groups separately allowed us to construct phylogenies for each group. Even then, phylogenies were better resolved for some groups than others (e.g. mammal and bird phylogenies were better than those for invertebrates – 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)^{24,63}, and greater variance for all five traits in accordance with the 'greater male variability' hypothesis¹⁴. More importantly, this analysis provides a baseline 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 variance⁶⁴. To correct

for the non-independence of species due to their shared evolutionary history we 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 birds⁶⁵) or using *TimeTree.org*⁶⁶. For the bird phylogeny, we used the Ericson tree backbone⁶⁷ 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 ;^{68,69}). We partitioned heterogeneity arising among species (I^2_{species}), studies (I^2_{study}), and due to phylogenetic heritability (I^2_{phylo} ⁶⁹). The total heterogeneity (I^2_{Total}), 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), life-histories (e.g. sex-biased dispersal is likely to affect exploration and activity), 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). 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 ran subset models for each personality trait type and included SSD. We only ran these subset models when there were 10 or more species for each personality type. There were too few data, and low heterogeneity, for reptiles/amphibians to run any models that included SSD (Table 3).

The studies included in our meta-analysis varied greatly in their design and there were a number of additional sources of non-independence within studies⁵³. 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 (Supplementary Tables S24-S22). The results presented in Tables 1-3 are robust and not due to non-independence.

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

Publication bias

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 $\ln\text{CVR}$. 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 results⁷⁰. 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 reported effect sizes. If precision has a significant influence, this is suggestive of publication bias. Precision was calculated as:

$$precision = \frac{1}{\sqrt{e_{vi}}}$$

Eq. 10

Where e_{vi} is the sampling variance of effect sizes' Hedge's g (Eq. 3-6) or $\ln\text{CVR}$ (Eq. 7-8).

Data availability

All data and code used in this study have been provided as Supplementary Material, but will also be uploaded to the Open Science Foundation when accepted: <https://osf.io/bwjyt/>

Author contributions

MDJ conceived the study, LMH collected data and conducted data analyses with DWAN. LMH wrote the first draft of the manuscript, and DWAN and MDJ edited and revised the final version. All authors have read and approved the final version of this manuscript submitted for publication.

553

554 **Competing interests**

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711

Parameters	Overall mean	95% CI	Prediction interval	<i>t</i> score	<i>p</i> -value	<i>n</i> effect sizes	<i>n</i> studies	<i>n</i> species
<i>SMD (Hedge's g - Mean)</i>								
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
<i>lnCVR (Variance)</i>								
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 1. Overall, there were no significant sex differences for either mean personality or for variability. 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	SMD mean	SMD 95%CI	SMD <i>p</i> -value	lnCVR mean	lnCVR 95%CI	lnCVR <i>p</i> -value	n effect sizes	n studies	n species
<i>Mammals</i>									
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
<i>Birds</i>									
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
<i>Reptiles / Amphibians</i>									
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
<i>Fish</i>									
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
<i>Invertebrates</i>									
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 2. Sex differences were significant for some trait types, within some taxa, but there was no consistent pattern. MLMR model summaries for each taxa with personality type as a fixed moderator. Values highlighted in bold indicate a significant difference ($\alpha < 0.05$) 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 studies	n species	n effect sizes
<i>Mammals</i>									
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			
<i>Birds</i>									
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			
<i>Fish</i>									
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			
<i>Invertebrates</i>									
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			

735

736 **Table 3. SSD explains sex differences in mean personality for two traits for mammals.**

737 Table shows subset analyses with personality trait type and SSD as moderator terms for four

738 of the five taxonomic groups. Estimates highlighted in bold indicate significant differences

739 between males and females. Positive estimates indicate that the mean and variability are

740 greater for males than females. Separate models were run for each trait type with SSD as a

741 moderator, therefore estimates show the personality trait mean when males and females are

742 the same size, and when males are larger than females. Only traits with 10 or more species

743 with SSD data were estimated.

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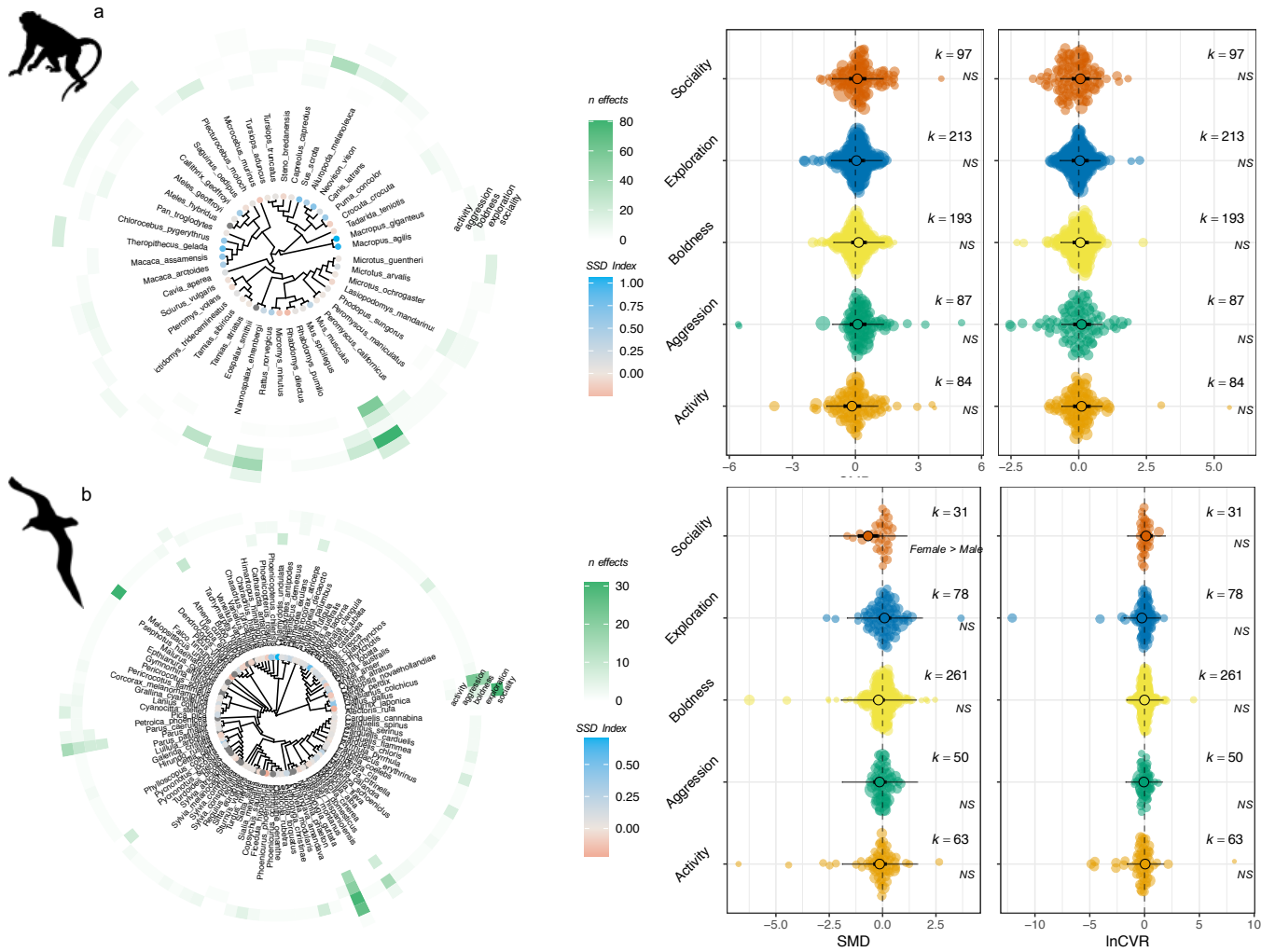


Figure 1. Phylogenetic relationships and orchard plots for a) mammals and b) birds. Node

colours reflect SSD ratios for each species (male-biased are blue, female-biased are red,

monomorphic are white and no data are grey) and heatmap data shows n effect sizes for each

personality trait type for each species. Orchard plots show total effect sizes (k) and mean

effect size for SMD and lnCVR meta-regression models with personality trait as a moderator

term. Thick bars are 95% CIs and thin bars are prediction intervals. Circle size reflects effect

size precision where larger circles have greater precision.

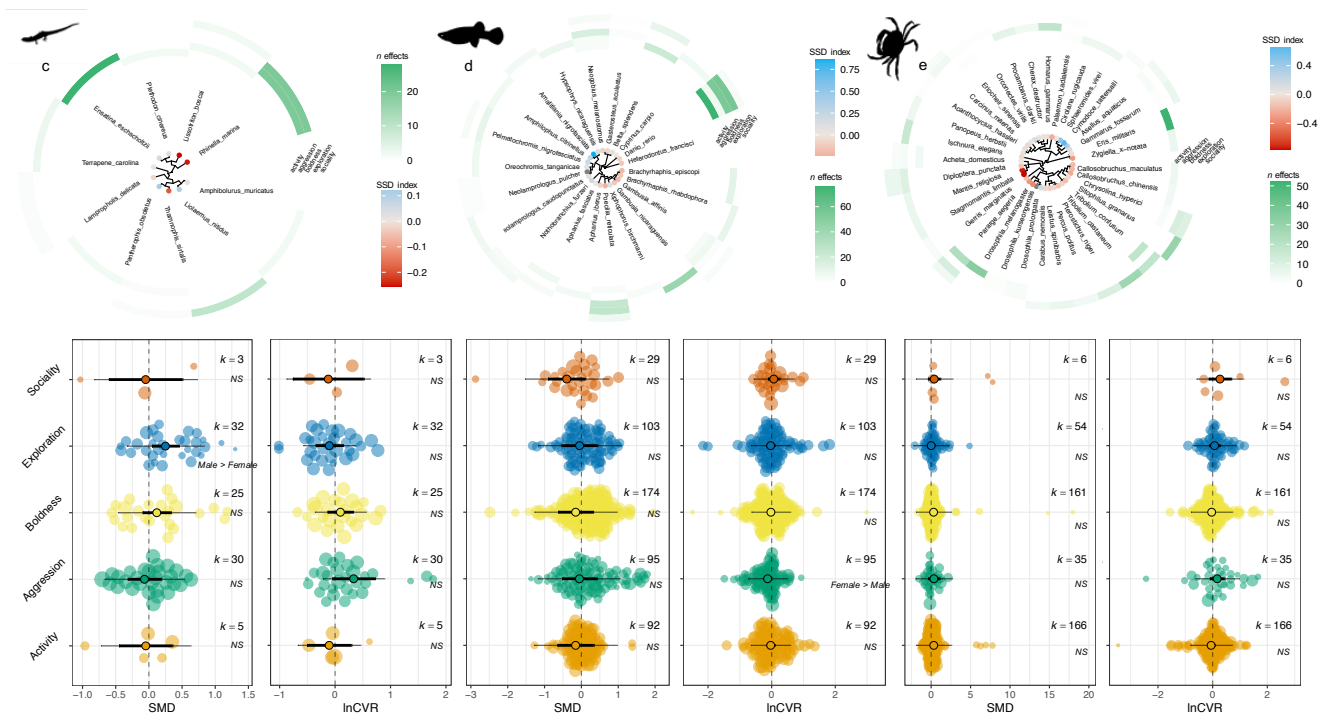


Figure 2. Phylogenetic relationships and orchard plots for c) reptiles and amphibians, d) fish and e) invertebrates. Node colours reflect SSD ratios for each species and heatmap data shows n effect sizes for each personality trait type for each species. Orchard plots show total effect sizes (k) and mean effect size for SMD and lnCVR meta-regression models with personality trait as a moderator term. Thick bars are 95% CIs and thin bars are prediction intervals. Circle size reflects effect size precision where larger circles have greater precision. Code and data used to generate Figures 1 & 2 are available in the accompanying Supplementary Material.

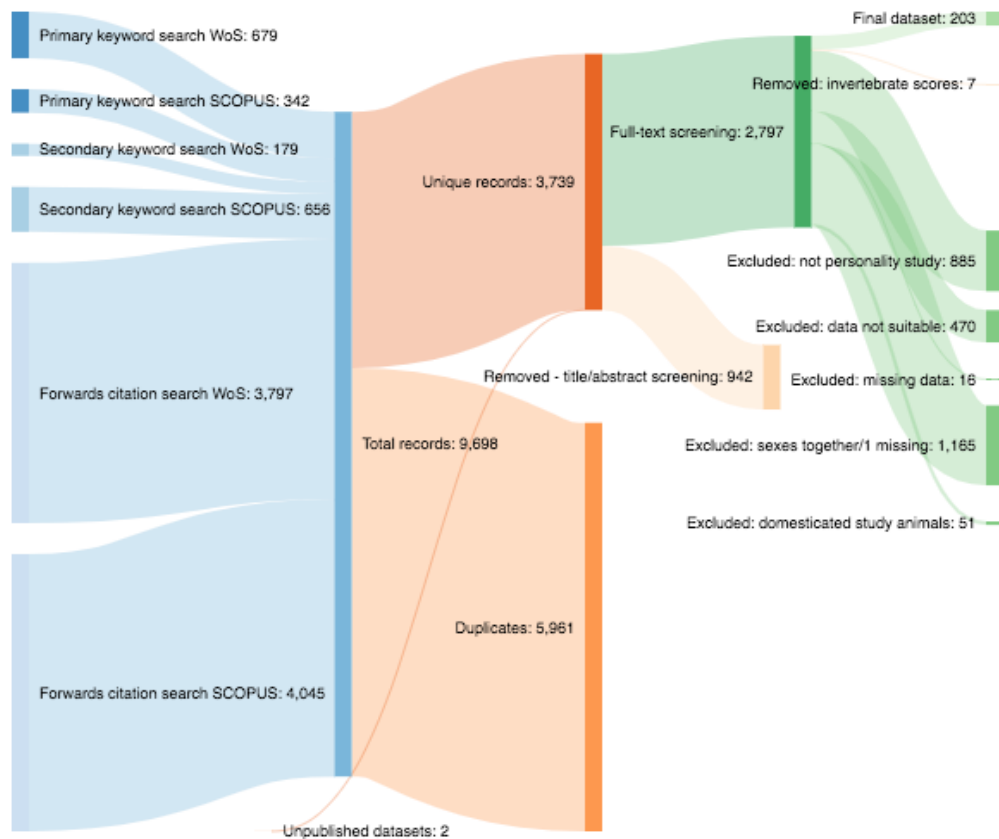


Figure 3. *PRISMA* diagram showing the process of finding, screening and including/excluding studies for this meta-analysis. See Supplementary Material accompanying this article for detailed keyword search terms.