

Title

Full title: Sex differences or similarities? Testing the ‘greater male variability’ hypothesis across the animal kingdom

Short title: Males are not always the variable sex

Authors

Lauren M. Harrison,^{1*} Daniel W. A. Noble,^{1†} Michael D. Jennions^{1†}

Affiliations

¹Division of Ecology and Evolution, Research School of Biology, 46 Sullivans Creek Road, The Australian National University, Canberra ACT 2600

[†]Authors contributed equally to this study

*Corresponding author: lauren.harrison@anu.edu.au

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 two significant sex differences in mean personality, but 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 see (1)). The causes and consequences of sex differences in behavioural variability have, however, been widely debated in the social sciences (2). For example, sex differences in variability in academic performance (3) or the classroom (4–6) have been linked to sex differences in variability in intelligence (7, 8), creativity (9), aggressiveness (10), personality (11) and, ultimately, brain structure (12). 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 STEM (13).

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 underplayed (2). 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 size (16–18). 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 agreeableness (21)), which are repeatable 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 sociability (22). 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 males (25). It favours individuals with greater expression of traits that increases the likelihood of obtaining mates (e.g. weapons, ornaments and coercive behaviours (26)), or fertilising eggs (27). 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 costs (28). 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 traits (28), 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 mechanisms (31). 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 chromosome (32). In contrast, males only express genes on the single, maternally inherited X chromosome. All else being equal, this should create more extreme phenotypes in males (33), hence greater variation among males than females. However, females are the heterogametic sex in some taxa, including birds, butterflies, and some fish and reptiles (34). If sex determination drives sex differences in variability then taxa with heterogametic females should exhibit greater variability in females (17).

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 SSD (35). 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.

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 Table S1). The effect size estimates from our basic meta-analytic intercept models all had high heterogeneity ($I^2_{\text{Total SMD}} > 0.70$; $I^2_{\text{Total lnCVR}} > 0.60$), while there was moderate-low heterogeneity for reptiles/amphibians ($I^2_{\text{Total SMD}} = 0.45$; $I^2_{\text{Total lnCVR}} = 0.01$) and for fish ($I^2_{\text{Total lnCVR}} = 0.49$). 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 (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 ($\bar{X}_{SMD} = -0.68$, 95% CIs: -1.16, -0.21; $p=0.005$), but less exploratory in reptiles/amphibians ($\bar{X}_{SMD} = 0.25$, 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, Fig. 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, Fig. 1 & 2 and 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 Table S3). 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 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 Table S3). 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 (Table S4).

Discussion

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 (Fig. 1 & 2). Indeed, the only significant sex difference reveals greater variability among females than males 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 (Table 3). 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.

Starting with Darwin (26), 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 traits (16). 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 females (18). In another cross-species study, variation in body size was significantly greater in males than females in taxa where males are the heterogametic sex, but the pattern was reversed in taxa where males are the homogametic sex (17).

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 individuals (19). 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* (20). 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 use a larger database of 226 species to show 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 work (19)), which has been hypothesised to arise, at least in mammals, due to the effect of females being at different

stages of their oestrus cycle (20). 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 variation (17). 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-linked (41), which might partially explain the strength of sex differences in variability found for both traits.

Sexual selection is another major biological explanation for greater variation among men than women in behavioural traits. 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 societies (42). Similarly, there is evidence that consistent, average levels of aggression elevate success during male-male competition (43). 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 traits (30). It is therefore relevant that we found no moderating effect of sexual size dimorphism, which is a standard proxy for the level of sexual selection on males (45), 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 care (46), and, in this context, there might therefore be equally strong selection on females as on males to be aggressive. Similarly, in group living animals, females often establish social hierarchies where dominance is maintained through aggressive interactions (47). 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 humans (48). 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 premature. Greater attention needs to be paid to the possible role of social factors that might select for a wider range of developmental pathways in boys than girls yielding greater behavioural variability in men than women (5).

Materials and Methods

General approach

We conducted a systematic review and meta-analysis to test the generality of the ‘greater male variability’ hypothesis across the animal kingdom. Comparisons of shared behavioural traits often provide conflicting evidence for the greater male variability hypothesis, so we chose to focus on animal personality as a way to compare shared behaviours that are likely very similar, and measured in similar ways, across many different species. For this synthesis, we extracted the raw means and error for personality and personality-like behaviours for both males and females from the primary literature (Fig 3). Recently, there has been a push for stricter definitions of personalities in animal behaviour studies (49). By definition, personality traits are repeatable (50), but few of the available personality studies reported repeatability, or did not cite previous work that 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, in particular when the test used was a common test of a personality trait, and also where the authors interpreted behaviours as ‘personalities’ (22, 50). While including studies that did not explicitly measure the repeatability of personality and personality-like behaviours could introduce potential problems with our interpretation, we felt that their inclusion allowed us to make much broader comparisons about the greater male variability hypothesis in shared behaviours in general.

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, 50). We ran primary and secondary keyword searches using the search strings shown in Table S5. 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, 50). 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, 50–52). 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 (53, 54). Consequently, studies that only report principle components or factor loadings were excluded (e.g. (19)). 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) (Fig. 3 and Supplementary Material).

In total, we identified 210 eligible articles with suitable data to calculate effect sizes (Fig. 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 1.0.0 (55) 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 Table S6). 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:

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

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

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 Material.

Effect sizes and sampling variances

To quantify sex differences in means and variances for personality traits we used unbiased standardised effect sizes. First, to quantify the difference between the sexes in the mean value of personality traits we calculated Hedges' g (sample size adjusted standardised mean difference (56)) as follows:

$$g = \frac{\bar{X}_M - \bar{X}_F}{SD_p} J, \quad (3)$$

$$SD_p = \sqrt{\frac{(N_M - 1)SD_M^2 + (N_F - 1)SD_F^2}{N_M + N_F - 2}}, \quad (4)$$

$$J = 1 - \frac{3}{4(N_M + N_F - 2) - 1} \quad (5)$$

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:

$$V_g = \left(\frac{N_M + N_F}{N_M N_F} + \frac{d^2}{2(N_M + N_F)} \right) J^2 \quad (6)$$

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 (53, 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) (53). 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 (53, 58). We calculated lnCVR and its associated sampling variance (s_{lnCVR}^2) as:

$$\ln\text{CVR} = \ln\left(\frac{CV_M}{CV_F}\right) + \frac{1}{2(N_M-1)} - \frac{1}{2(N_F-1)}, \quad (7)$$

$$s_{lnCVR}^2 = \frac{SD_M^2}{N_M \bar{X}_M^2} + \frac{1}{2(N_M-1)} - 2\rho_{\ln\bar{X}_M^2, \overline{SD}_M^2} \sqrt{\frac{SD_M^2}{N_M \bar{X}_M^2} \frac{1}{2(N_M-1)}} + \frac{SD_F^2}{N_F \bar{X}_F^2} + \frac{1}{2(N_F-1)} - 2\rho_{\ln\bar{X}_F^2, \overline{SD}_F^2} \sqrt{\frac{SD_F^2}{N_F \bar{X}_F^2} \frac{1}{2(N_F-1)}} \quad (8)$$

where CV_M and CV_F are SD_M/\bar{X}_M and SD_F/\bar{X}_F , respectively; and $\rho_{\ln\bar{X}_M^2, \overline{SD}_M^2}$ and $\rho_{\ln\bar{X}_F^2, \overline{SD}_F^2}$ are the correlation between the logged means and standard deviations of males and females respectively. A positive value of lnCVR indicates that males are variable than females.

Moderator variables

We extracted information on factors that differed among studies where we had an *a priori* expectation that they might moderate the magnitude and/or direction of the effect size (19). Specifically, we recorded the taxa ('invertebrates', 'fish', 'amphibians', 'reptiles', 'birds', 'mammals'), the age of individuals ('juvenile' or 'adult'), whether the study population was from the lab (captive breed) or the wild, whether the behaviours were measured in the lab or field, and whether the data was collected in an experiment or during natural behaviour of the subject ('experimental' or 'observational'). Most importantly, we generated two moderator variables to quantify the strength of sexual selection. First, we quantified the degree of sexual size dimorphism (SSD), which is often strongly correlated with indicators of the strength of sexual selection (35). We calculated SSD as the ratio of male to female mean body length, mass or the size of another focal, dimorphic trait (e.g. wing length) using the following index of SSD (59):

$$\text{SSD index} = \left(\frac{\bar{X}_{M_{bodysize}}}{\bar{X}_{F_{bodysize}}}\right) - 1 \quad (9)$$

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

0 males are larger than females; and 2) comparison of SSD across a wide range of absolute
1 size measures. Larger values of the SSD index are interpreted as species in which there is
2 increasingly stronger sexual selection on males. Where body size measures for males and
3 females were not reported in the research article, we searched *Web of Science*, *Scopus* and
4 *Google Scholar* using the search terms: “species name” AND male AND female AND
5 body size OR length. For birds, we first searched *CRC Handbook of Avian Body Masses*
6 (60) and the online reference database *Birds of the World* (birdsoftheworld.org; accessed
7 via an ANU library subscription in 2019) for body size measures. We then used data from
8 located studies to calculate the SSD index.

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

5
6 Based on the number of available studies for different levels of the prospective moderators
7 (age, population source, test location, experimental/observational), or the level of
8 subjectivity required to categorise species (mating system), we decided upon completion
9 of data collection that the only moderators we would formally analyse using a null
0 hypothesis framework for their influence on the effect sizes were the SSD index and taxa.
1 The relationships between the other moderators and the effect sizes are presented in the
2 Supplementary Material, but these should be treated as strictly exploratory analyses.

3 4 *Statistical analysis*

5 We modelled the effect sizes Hedge’s g and $\ln\text{CVR}$ using multi-level meta-analytic
6 (MLMA) models (intercept only models that consider random effects) and then ran multi-
7 level meta-regression (MLMR) models (including fixed effect moderators) in R version
8 3.5.1 (61) using the package *metafor* (version 2.4.0) (62). We ran separate models for each
9 of our five taxonomic groups, namely: birds, mammals, fish, invertebrates and
0 reptiles/amphibians (combined due to low sample sizes). Although we were interested in
1 whether sex differences varied across these taxonomic groups, the available sample sizes
2 generally precluded running models with taxa as a moderator and would have resulted in
3 an overly complicated interpretation. Furthermore, the diversity of taxa made it
4 challenging to create a full phylogeny that included all taxa to account for evolutionary
5 relationships and non-independence (54). Focusing on broad taxonomic groups separately
6 allowed us to construct phylogenies for each group. Even then, phylogenies were better
7 resolved for some groups than others (e.g. mammal and bird phylogenies were better than
8 those for invertebrates – see below).

9
0 We first estimated the overall evidence for a sex difference in the mean and variance
1 across all personality traits using MLMA models (Table 1). This analysis is based on the
2 simple premise that we predict males will show larger trait values for personality traits
3 (with the possible exception of sociality) (24, 63), and greater variance for all five traits in
4 accordance with the ‘greater male variability’ hypothesis (14). More importantly, this
5 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 variance (64). 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 birds (65)) or using *TimeTree.org* (66). For the bird phylogeny, we used the Ericson tree backbone (67) 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 $\ln\text{CVR}$ 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 studies (54). 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 (Tables S7-S8). 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 results (70). 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:

$$precision = \frac{1}{\sqrt{e_{vi}}} \quad (10)$$

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

H2: Supplementary Materials

Table S1 – model output summaries of intercept-only meta-analysis models for each of the five taxonomic groups, for means (SMD) and variability ($\ln\text{CVR}$).

Table S2 – model output summaries of multi-level meta-regression models for each of the five taxonomic groups with personality trait type as a moderator (for both SMD and $\ln\text{CVR}$).

Table S3 – subset model summaries for multi-level meta-regression models with SSD index as a moderator, for each taxonomic group / personality trait type with enough available data.

Table S4 – summary of our full model (multi-level meta-regression models) with precision included as a moderator term to look for publication bias (in both SMD and $\ln\text{CVR}$ effect sizes).

Table S5 – keyword search terms utilised in our primary and secondary database searches.

Table S6 – contrast model summaries comparing effect sizes calculated from scores with effect sizes that are normally-distributed (including transformed effect sizes).

Table S7 – Sensitivity models. **D** matrix models for intercept-only models (presented in Table 1) where the correlation between personality traits measured on the same individuals within studies are set at $r = 0.8$.

Table S8 - Sensitivity models. **D** matrix models for multi-level meta-regression models with personality trait type (presented in Table 2) where the correlation between personality traits measured on the same individuals within studies are set at $r = 0.8$.

Table S9 – table of studies included in our final dataset (refs 71-271 in bold, indicated by *)

Data files S10-13

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Figures and Tables

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 | Overall mean | 95% CIs | 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 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% CIs | SMD <i>p</i> -value | lnCVR mean | lnCVR 95% CIs | 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 |

1 **Table 3. SSD explains sex differences in mean personality for two traits for mammals.** Table
2 shows subset analyses with personality trait type and SSD as moderator terms for four of the five
3 taxonomic groups. Estimates highlighted in bold indicate significant differences between males
4 and females. Positive estimates indicate that the mean and variability are greater for males than
5 females. Separate models were run for each trait type with SSD as a moderator, therefore
6 estimates show the personality trait mean when males and females are the same size, and when
7 males are larger than females. Only traits with 10 or more species with SSD data were estimated.

| Parameters | SMD mean | SMD 95% CIs | SMD <i>p</i> -value | lnCVR mean | lnCVR 95% CIs | lnCVR <i>p</i> -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 | | | |

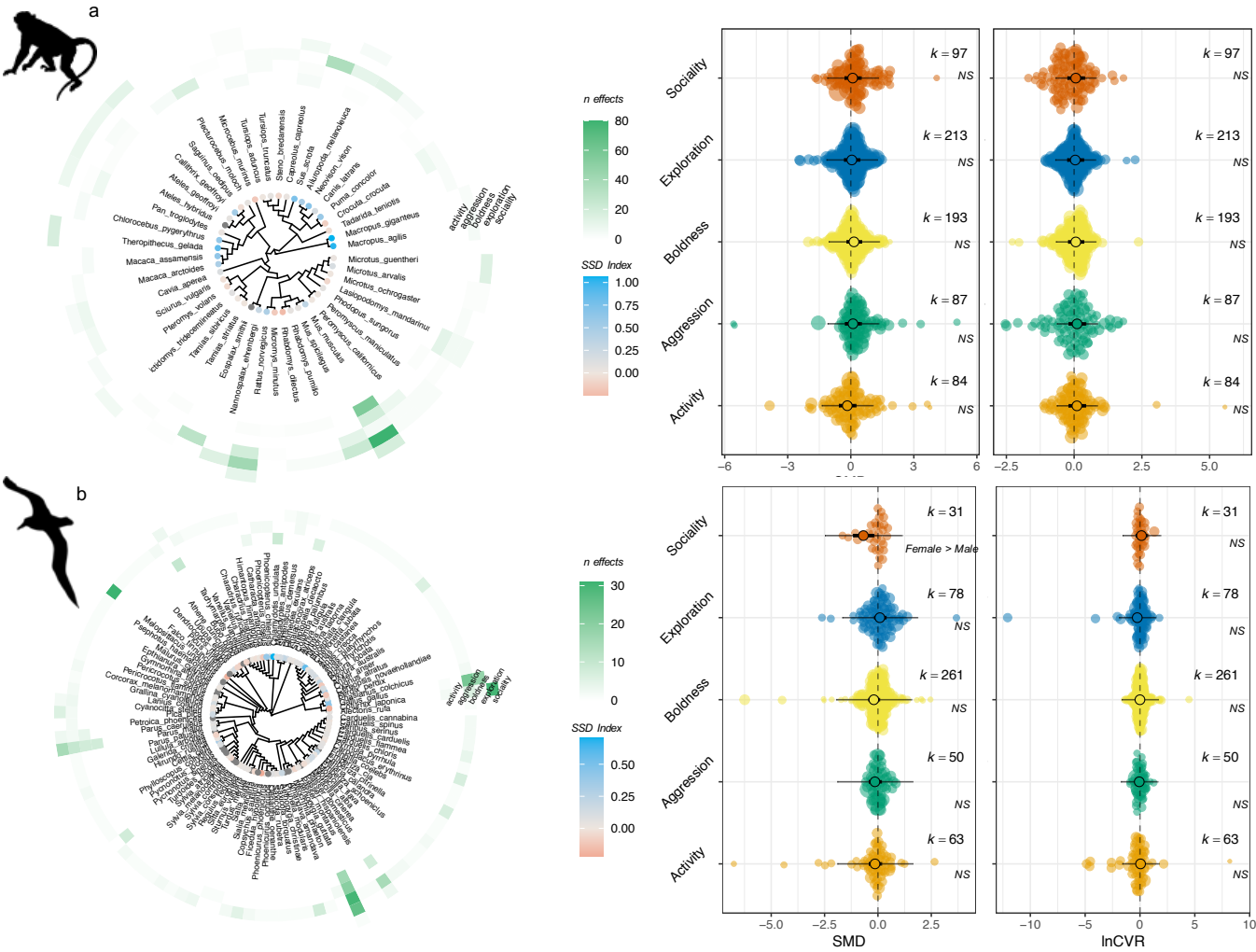
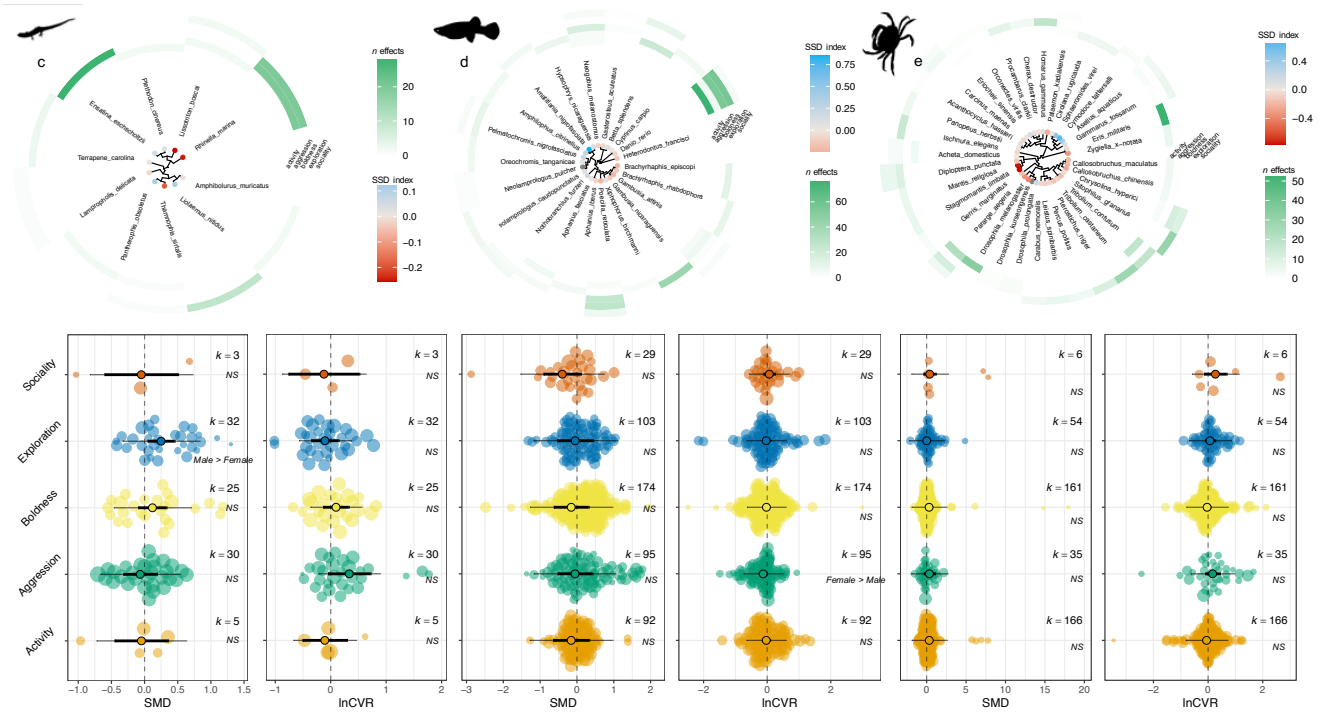


Fig. 1. Sex differences in means and variability for the five personality traits for endotherms. Phylogenetic relationships and orchard plots for (A) mammals and (B) birds. Node colours reflect SSD ratios for each species (male-biased are blue, female-biased are red, monomorphic are white and no data 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.



1

2 **Fig. 2. Sex differences in means and variability for the five personality traits for ectotherms.**
3 Phylogenetic relationships and orchard plots for (C) reptiles and amphibians, (D) fish and (E)
4 invertebrates. Node colours reflect SSD ratios for each species and heatmap data shows n effect
5 sizes for each personality trait type for each species. Orchard plots show total effect sizes (k) and
6 mean effect size for SMD and lnCVR meta-regression models with personality trait as a
7 moderator term. Thick bars are 95% CIs and thin bars are prediction intervals. Circle size reflects
8 effect size precision where larger circles have greater precision. Code and data used to generate
9 Figures 1 & 2 are available in the accompanying Supplementary Material.

0

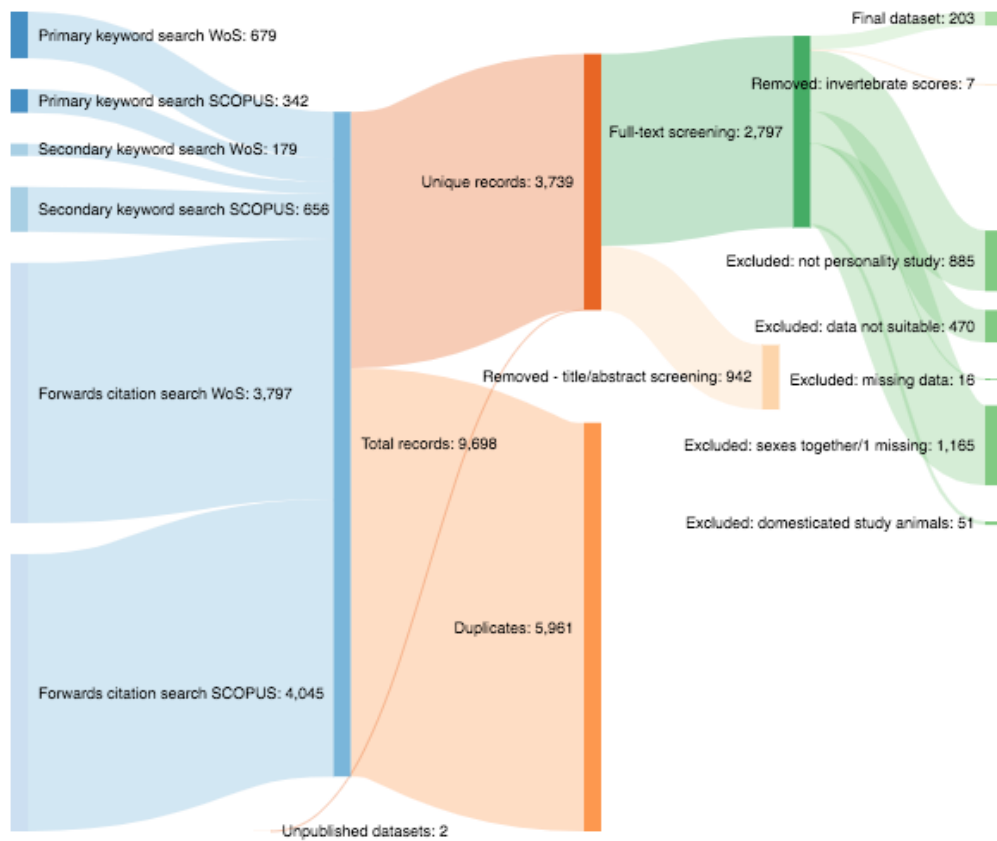


Fig. 3. PRISMA diagram of the literature search process. The process of finding, screening and including/excluding studies for this meta-analysis. See Table S8 for detailed keyword search terms used to locate studies.

Supplementary Materials

1. *Data collection – mating system and parental care moderator terms*

We searched *ISI Web of Science*, *Scopus* and *Google Scholar* using the search terms: “species name” AND “mating system” for mating system and “species name” AND “parental care” for parental care. For birds, we also searched the online reference database *Birds of the World* (birdsoftheworld.org; accessed via an ANU library subscription in 2019) by searching “species name”. We noted whether the mating system of the species was characterised by ‘multiple mating’ or ‘monogamy’, and whether the species provided ‘maternal’, ‘paternal’, ‘biparental’, ‘cooperative’ or ‘no care’. However, after data collection we decided to drop parental care from subsequent analysis because 1) we did not have enough data for enough species to run our proposed meta-regression models and 2) data quality was questionable. The location of data collected for both parental care and mating system (and body sizes for SSD) are provided in the data file ‘sexual_selection.xlsx’ here: <https://osf.io/bwjyt/>

2. *Excluding studies and effect sizes*

After full-text screening, we were left with a total of $n=247$ studies. However, $n=29$ studies were excluded from this initial inclusion list because behaviours did not really fit into personality categorisation, or were missing some key data required to calculate effect sizes. Another $n=8$ studies were excluded before analysis was conducted because studies were missing data required to calculate effect sizes, producing NAs. This left us with a total of $n=210$ studies in our final dataset.

Before analysis, we removed $n=2$ effect sizes (both from the same study on invertebrates) that were extremely large outliers. We also had $n=24$ effect sizes in our dataset that were more physiological than behavioural (i.e. breathing rate, max. heart rate after capture etc.). We decided to remove these effect sizes before running models, which reduced the total number of effect sizes, but did not change the number of studies or species in our final dataset.

While we decided not to email authors for missing data (i.e. sample sizes, error type, additional information), we did obtain sample sizes for males and females in study P077 via email correspondence with a co-author of the study.

Additionally, there were 3 studies in our dataset (P172, P210 and P231) that we were concerned might have issues with data duplication/unreliability. LMH checked the retraction database retractiondatabase.org regularly during data analysis to check if these studies had been either retracted or flagged for concern. As of 31 August 2020, none of the 3 studies had been retracted, nor had any other concerns been raised, so we decided to keep these studies in our final dataset.

3. *Score data*

We performed data transformations on latency data and proportional data in order to meet assumptions about normality. However, we were unable to adjust score data, and therefore assumed that scores were normally distributed. Scores did not make up a large proportion of our effect size dataset, but we decided to run contrast meta-analysis models to check whether

data composed of scores were significantly different from the rest of our dataset. Summaries of these models are shown in Table S6.

Score data - invertebrates

Effect sizes calculated from scores were significantly different from the rest of the dataset (including transformed latency and proportion data) for mean differences in personality for invertebrates only (intercept: $\bar{X}_{SMD} = 0.30$, 95% CIs: 0.02, 0.57, $t = 2.12$, $p = 0.03$; score: $\bar{X}_{SMD} = -0.29$, 95% CIs: -0.57, -0.02, $t = -2.11$, $p = 0.04$). Invertebrates had the most score data of any taxonomic group ($n = 61$ effect sizes). We therefore decided to exclude these scores from our invertebrate dataset and rerun our models. Study ID of these removed studies were P081, P103, P142, P153, P172, P199 and P210. All invertebrate model tables and figures report data after scores were removed.

4. Calculating I^2

We extracted I^2 from our meta-analytic intercept-only models (see Table S1) using the following equation:

$$\sigma_t^2 = \sigma_a^2 + \sigma_s^2 + \sigma_u^2 + \sigma_e^2 + \sigma_m^2$$

Where σ_t^2 is the total variance, σ_a^2 is the phylogenetic variance, σ_s^2 is the between-study variance, σ_u^2 is the species-specific variance, σ_e^2 is the study-specific variance (observation-level random effect), and σ_m^2 is the remaining within-study sampling variance (random effects) (69). Further, we can then partition I^2 to calculate study-level I^2 and species-level I^2 (I_s^2 and I_u^2 , respectively) (69):

$$I_s^2 = \sigma_s^2 / \sigma_t^2 ,$$

$$I_u^2 = \sigma_u^2 / \sigma_t^2$$

Finally, we can determine the strength of phylogenetic variance using the equation:

$$H^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_s^2 + \sigma_u^2 + \sigma_e^2)$$

Where $H^2 = 0$ there is no phylogenetic signal, but when $H^2 = 1$ there is a strong effect of phylogeny on heterogeneity (69).

5. Exploratory analysis

We extracted information on factors that differed among studies where we had an *a priori* expectation that they might moderate the magnitude and/or direction of the effect size. For mating system, we followed methods similar to those used to obtain SSD measures. Where mating system was not reported in the research article, we searched *Web of Science*, *Scopus* and *Google Scholar* using the search terms: “species name” AND “mating system”. For birds, we first searched the online reference database *Birds of the World* (birdsoftheworld.org; accessed via an ANU library subscription in 2019). Initially we wanted to categorise mating

system into the following: “monogamous”, “polyandrous”, “polygynous”, or “promiscuous”. However, it was difficult to find studies that agreed on mating system definitions for many species, so we collapsed our mating system categories into just “monogamous” or “multiple mating”. The location of data collected for mating system is provided in the data file ‘sexual_selection.xlsx’.

6. *Exploratory analysis - results*

Mating System

Monogamous and multiple mating systems were not significantly different from each other for means or variability for any of the taxonomic groups.

Age

Adults and juveniles were not significantly different from each other for means or variability for any of the taxonomic groups.

Population

Fish from the wild had greater differences in variability than fish from lab populations (intercept: $\bar{X}_{lnCVR} = -0.09$, 95% CIs: -0.18, -0.01, $t = -2.11$, $p = 0.04$; lab: $\bar{X}_{lnCVR} = 0.08$, 95% CIs: -0.02, 0.19, $t = 1.55$, $p = 0.12$), but not for mean personality differences, and not for any other taxonomic group.

Study environment

Studies conducted in the lab were significantly different to field studies for mammals (intercept: $\bar{X}_{SMD} = 0.24$, 95% CIs: -0.10, 0.57, $t = 1.38$, $p = 0.17$; lab: $\bar{X}_{SMD} = -0.30$, 95% CIs: -0.56, -0.04, $t = -2.26$, $p = 0.02$), but not for variability, and not for any other taxonomic group.

Study type

Effect sizes from observational studies were significantly different from experimental studies for mammals (intercept: $\bar{X}_{SMD} = 0.00$, 95% CIs: -0.21, 0.22, $t = 0.04$, $p = 0.97$; observation: $\bar{X}_{SMD} = 0.38$, 95% CIs: 0.12, 0.64, $t = 2.81$, $p = 0.005$), but not for variability, and not for any other taxonomic group for which comparisons could be made.

7. **D** matrices – results

Intercept only models

Regardless of whether the correlation between personality traits was set to either $r = 0.3$, 0.5 or 0.8 (i.e. to control for traits that were measured on the same individuals within the same study), there remained no significant sex difference between either the mean or the variability for personality overall, for any of the five taxonomic groups (see Table S7). We therefore interpreted our initial intercept only models without **D** matrices (Table S1).

Personality trait models - mean differences

Female birds were more social than males, while male reptiles/amphibians were more explorative than females (at each of the levels of ρ ; see Table S8 for $r = 0.8$). These significant sex differences, and their direction, were consistent with those from models without any **D** matrix (Table S2). However, male invertebrates were more active than females when $r = 0.3$, when $r = 0.5$, and when $r = 0.8$ (Table S8). This significant sex difference, for invertebrates, was not found in our initial MLMR personality models (but was marginally significant, see Table S2). However, since we also observed significant publication bias in our invertebrate data (Table S4), we therefore decided to interpret and report our more conservative mean model estimates.

Personality trait models - variability

Adjusting the levels of ρ for variability did not significantly change the results obtained from initial MLMR personality models for any of the taxonomic groups. Importantly, female fish remained significantly more variable than males for aggressive behaviour, regardless of the level of ρ (Table S8).

SSD and personality traits

Adjusting the levels of ρ for both means and for variability did change some effect sizes and made them more significant, but only for some traits, and only for some taxonomic groups (reptiles / amphibians, and invertebrates). However, our reptiles / amphibians taxonomic group didn't have enough data to support meta-regression models, and our invertebrate group had significant publication bias (Table S4), so we chose to interpret and present our more conservative models that did not include **D** matrices.

Supplementary Tables

Table S1. Intercept-only random effects meta-analysis model output for each of the five taxonomic groups comparing males and females for mean differences (SMD) and for variability (lnCVR). Table also shows I^2 measures of heterogeneity for each of the random effects included in the models. Q scores are another test of heterogeneity, but we only report I^2 .

| | | | | | |
|-----------------|-----------------|----------------|----------------------|----------------------------|----------------|
| Birds | | | | | |
| SMD | | | | | |
| Q=2804.93 | P<0.0001 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>I²</i> | <i>95% CIs</i> | <i>n</i> |
| Study ID | 0.59 | 0.77 | 0.73 | 0.63, 0.80 | 50 |
| Species Name | 0 | 0.01 | 0 | 0, 0 | 106 |
| Obs | 0.16 | 0.40 | | | 483 |
| Phylo | | | 0 | 0, 0 | |
| Total | | | 0.93 | 0.90, 0.95 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | -0.14 | -0.36, 0.09 | -1.17 | -1.82, 1.57 | 0.24 |
| lnCVR | | | | | |
| Q=3820.60 | P<0.0001 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>I²</i> | <i>95% CIs</i> | <i>n</i> |
| Study ID | 0.01 | 0.12 | 0.02 | 0.01, 0.02 | 50 |
| Species Name | 0.36 | 0.60 | 0.44 | 0.37, 0.51 | 106 |
| Obs | 0.40 | 0.63 | | | 483 |
| Phylo | | | 0.47 | 0.39, 0.54 | |
| Total | | | 0.94 | 0.94, 0.95 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | -0.14 | -0.65, 0.37 | -0.56 | -1.94, 1.64 | 0.58 |
| Fish | | | | | |
| SMD | | | | | |
| Q=1385.84 | P<0.0001 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>I²</i> | <i>95% CIs</i> | <i>n</i> |
| Study ID | 0.04 | 0.21 | 0.14 | 0.09, 0.19 | 44 |
| Species Name | 0.04 | 0.20 | 0.13 | 0.07, 0.20 | 22 |
| Obs | 0.13 | 0.36 | | | 493 |
| Phylo | | | 0.19 | 0.11, 0.29 | |
| Total | | | 0.70 | 0.66, 0.73 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | -0.04 | -0.35, 0.28 | -0.24 | -1.00, 0.93 | 0.81 |
| lnCVR | | | | | |
| Q=924.06 | P<0.0001 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>I²</i> | <i>95% CIs</i> | <i>n</i> |
| Study ID | 0.01 | 0.09 | 0.04 | 0.03, 0.06 | 44 |
| Species Name | 0.00 | 0.00 | 0 | 0, 0 | 22 |
| Obs | 0.08 | 0.29 | | | 493 |
| Phylo | | | 0 | 0, 0 | |
| Total | | | 0.49 | 0.46, 0.52 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | -0.04 | -0.09, 0.01 | -1.44 | -0.64, 0.56 | 0.15 |
| Inverts | | | | | |
| SMD | | | | | |
| Q=2678.23 | P<0.0001 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>I²</i> | <i>95% CIs</i> | <i>n</i> |
| Study ID | 0.90 | 0.95 | 0.70 | 0.60, 0.79 | 37 |
| Species Name | 0 | 0 | 0 | 0, 0 | 36 |
| Obs | 0.31 | 0.56 | | | 422 |
| Phylo | | | 0 | 0, 0 | |
| Total | | | 0.96 | 0.94, 0.97 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | 0.30 | -0.02, 0.62 | 1.82 | -1.89, 2.48 | 0.07 |

| | | | | | |
|------------------------------|-----------------|----------------|----------------------|----------------------------|----------------|
| <i>lnCVR</i> | | | | | |
| Q=1459.70 | | P<0.0001 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>I²</i> | <i>95% CIs</i> | <i>n</i> |
| Study ID | 0.04 | 0.20 | 0.20 | 0.13, 0.28 | 37 |
| Species Name | 0 | 0.06 | 0.02 | 0.01, 0.02 | 36 |
| Obs | 0.11 | 0.33 | | | 422 |
| Phylo | | | 0.02 | 0.01, 0.03 | |
| Total | | | 0.76 | 0.74, 0.79 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | 0.00 | -0.11, 0.10 | -0.04 | -0.77, 0.76 | 0.97 |
| Mammals | | | | | |
| <i>SMD</i> | | | | | |
| Q=2218.15 | | P<0.0001 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>I²</i> | <i>95% CIs</i> | <i>n</i> |
| Study ID | 0.10 | 0.31 | 0.23 | 0.16, 0.29 | 61 |
| Species Name | 0.08 | 0.29 | 0.19 | 0.13, 0.26 | 45 |
| Obs | 0.16 | 0.39 | | | 674 |
| Phylo | | | 0.24 | 0.16, 0.33 | |
| Total | | | 0.78 | 0.75, 0.81 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | 0.08 | -0.28, 0.45 | 0.44 | -1.10, 1.27 | 0.66 |
| <i>lnCVR</i> | | | | | |
| Q=1074.96 | | P<0.0001 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>I²</i> | <i>95% CIs</i> | <i>n</i> |
| Study ID | 0.03 | 0.18 | 0.17 | 0.12, 0.22 | 61 |
| Species Name | 0.05 | 0.22 | 0.25 | 0.18, 0.34 | 45 |
| Obs | 0.03 | 0.19 | | | 674 |
| Phylo | | | 0.43 | 0.31, 0.53 | |
| Total | | | 0.60 | 0.55, 0.65 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | 0.07 | -0.20, 0.34 | 0.51 | -0.64, 0.79 | 0.61 |
| Reptiles / Amphibians | | | | | |
| <i>SMD</i> | | | | | |
| Q=163.37 | | P<0.0001 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>I²</i> | <i>95% CIs</i> | <i>n</i> |
| Study ID | 0.03 | 0.17 | 0.15 | 0.06, 0.28 | 11 |
| Species Name | 0 | 0.01 | 0 | 0, 0 | 10 |
| Obs | 0.05 | 0.23 | | | 95 |
| Phylo | | | 0 | 0, 0 | |
| Total | | | 0.45 | 0.36, 0.54 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | 0.07 | -0.08, 0.22 | 0.94 | -0.52, 0.67 | 0.35 |
| <i>lnCVR</i> | | | | | |
| Q=77.72 | | P=0.89 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>I²</i> | <i>95% CIs</i> | <i>n</i> |
| Study ID | 0 | 0.02 | 0 | 0, 0 | 11 |
| Species Name | 0 | 0.02 | 0 | 0, 0.01 | 10 |
| Obs | 0 | 0 | | | 95 |
| Phylo | | | 0.65 | 0.34, 0.87 | |
| Total | | | 0.01 | 0.00, 0.01 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | 0.05 | -0.04, 0.14 | 1.13 | -0.06, 0.15 | 0.26 |

Table S2. Multi-level meta-regression model output for each of the five taxonomic groups with personality trait type as a moderator variable. Here we compare mean differences (SMD) and variability (lnCVR) between males and females for each of the five personality trait types. F scores are tests of how well the moderator, trait type, explains variance.

| | | | | | |
|-------------------|----------|--------------|---------|---------------------|---------|
| Birds | | | | | |
| SMD | | | | | |
| QE=2670.89 | P<0.0001 | | | | |
| F=3.76 | P=0.002 | | | | |
| Variance | Estimate | SQRT | n | | |
| Study ID | 0.59 | 0.77 | 50 | | |
| Species Name | 0 | 0.01 | 106 | | |
| Obs | 0.16 | 0.40 | 483 | | |
| Personality Trait | Estimate | 95% CIs | t-score | Prediction Interval | p-value |
| Activity | -0.14 | -0.43, 0.15 | -0.93 | -1.90, 1.62 | 0.35 |
| Aggression | -0.14 | -0.43, 0.14 | -0.97 | -1.90, 1.62 | 0.33 |
| Boldness | -0.19 | -0.44, 0.06 | -1.50 | -1.95, 1.56 | 0.13 |
| Exploration | 0.09 | -0.18, 0.36 | 0.66 | -1.67, 1.85 | 0.51 |
| Sociality | -0.68 | -1.16, -0.21 | -2.81 | -2.48, 1.12 | 0.005** |
| lnCVR | | | | | |
| QE=3711.80 | P<0.0001 | | | | |
| F=1.17 | P=0.32 | | | | |
| Variance | Estimate | SQRT | n | | |
| Study ID | 0.31 | 0.55 | 50 | | |
| Species Name | 0 | 0 | 106 | | |
| Obs | 0.39 | 0.62 | 483 | | |
| Personality Trait | Estimate | 95% CIs | t-score | Prediction Interval | p-value |
| Activity | 0.05 | -0.24, 0.34 | 0.36 | -1.61, 1.71 | 0.72 |
| Aggression | -0.07 | -0.39, 0.25 | -0.41 | -1.74, 1.60 | 0.68 |
| Boldness | -0.01 | -0.23, 0.22 | -0.04 | -1.66, 1.65 | 0.97 |
| Exploration | -0.25 | -0.50, 0.01 | -1.92 | -1.91, 1.41 | 0.06 |
| Sociality | 0.14 | -0.38, 0.66 | 0.53 | -1.58, 1.86 | 0.60 |
| Fish | | | | | |
| SMD | | | | | |
| QE=1347.79 | P<0.0001 | | | | |
| F=1.80 | P=0.11 | | | | |
| Variance | Estimate | SQRT | n | | |
| Study ID | 0.03 | 0.17 | 44 | | |
| Species Name | 0.10 | 0.32 | 22 | | |
| Obs | 0.13 | 0.37 | 493 | | |
| Personality Trait | Estimate | 95% CIs | t-score | Prediction Interval | p-value |
| Activity | -0.16 | -0.65, 0.33 | -0.63 | -1.28, 0.97 | 0.53 |
| Aggression | -0.05 | -0.52, 0.42 | -0.22 | -1.17, 1.06 | 0.83 |
| Boldness | -0.16 | -0.63, 0.32 | -0.65 | -1.27, 0.96 | 0.52 |
| Exploration | -0.05 | -0.54, 0.44 | -0.20 | -1.17, 1.07 | 0.84 |
| Sociality | -0.40 | -1.53, 0.73 | -1.55 | -1.53, 0.73 | 0.12 |
| lnCVR | | | | | |
| QE=915.16 | P<0.0001 | | | | |
| F=1.14 | P=0.34 | | | | |
| Variance | Estimate | SQRT | n | | |
| Study ID | 0.01 | 0.10 | 44 | | |
| Species Name | 0 | 0 | 22 | | |
| Obs | 0.08 | 0.29 | 493 | | |
| Personality Trait | Estimate | 95% CIs | t-score | Prediction Interval | p-value |
| Activity | -0.03 | -0.16, 0.09 | -0.49 | -0.65, 0.58 | 0.63 |
| Aggression | -0.13 | -0.25, -0.01 | -2.10 | -0.74, 0.49 | 0.04* |

| | | | | | |
|------------------------------|-----------------|----------------|----------------|----------------------------|----------------|
| Boldness | -0.02 | -0.11, 0.06 | -0.54 | -0.63, 0.59 | 0.59 |
| Exploration | -0.03 | -0.65, 0.58 | -0.50 | -0.65, 0.58 | 0.62 |
| Sociality | 0.07 | -0.56, 0.69 | 0.72 | -0.56, 0.69 | 0.47 |
| Inverts | | | | | |
| SMD | | | | | |
| QE=2657.20 | P<0.0001 | | | | |
| F=1.46 | P=0.02 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.92 | 0.96 | 37 | | |
| Species Name | 0 | 0 | 36 | | |
| Obs | 0.32 | 0.56 | 422 | | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| Activity | 0.33 | -0.04, 0.70 | 1.77 | -1.89, 2.55 | 0.08 |
| Aggression | 0.35 | -0.36, 1.06 | 0.97 | -1.95, 2.65 | 0.33 |
| Boldness | 0.31 | -0.05, 0.67 | 1.70 | -1.91, 2.53 | 0.09 |
| Exploration | 0.00 | -0.44, 0.45 | 0.02 | -2.23, 2.37 | 0.98 |
| Sociality | 0.39 | -0.38, 1.16 | 1.00 | -1.93, 2.71 | 0.32 |
| lnCVR | | | | | |
| QE=1427.81 | P<0.0001 | | | | |
| F=1.03 | P=0.40 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.03 | 0.18 | 37 | | |
| Species Name | 0 | 0 | 36 | | |
| Obs | 0.09 | 0.30 | 422 | | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| Activity | -0.06 | -0.19, 0.08 | -0.83 | -0.82, 0.70 | 0.40 |
| Aggression | 0.17 | -0.10, 0.43 | 1.22 | -0.63, 0.96 | 0.22 |
| Boldness | -0.04 | -0.15, 0.08 | -0.61 | -0.79, 0.72 | 0.55 |
| Exploration | 0.07 | -0.12, 0.26 | 0.73 | -0.70, 0.84 | 0.47 |
| Sociality | 0.27 | -0.14, 0.68 | 1.29 | -0.59, 1.12 | 0.20 |
| Mammals | | | | | |
| SMD | | | | | |
| QE=2158.51 | P<0.0001 | | | | |
| F=1.40 | P=0.22 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.13 | 0.36 | 61 | | |
| Species Name | 0.07 | 0.26 | 45 | | |
| Obs | 0.15 | 0.39 | 674 | | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| Activity | -0.17 | -0.56, 0.23 | -0.84 | -1.38, 1.05 | 0.40 |
| Aggression | 0.10 | -0.27, 0.48 | 0.55 | -1.10, 1.31 | 0.59 |
| Boldness | 0.15 | -0.20, 0.50 | 0.85 | -1.05, 1.35 | 0.39 |
| Exploration | 0.05 | -0.31, 0.41 | 0.26 | -1.56, 1.25 | 0.79 |
| Sociality | 0.09 | -0.29, 0.47 | 0.46 | -1.12, 1.30 | 0.64 |
| lnCVR | | | | | |
| QE=1044.60 | P<0.0001 | | | | |
| F=0.26 | P=0.93 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.03 | 0.18 | 61 | | |
| Species Name | 0 | 0 | 45 | | |
| Obs | 0.09 | 0.30 | 674 | | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| Activity | 0.10 | -0.20, 0.41 | 0.67 | -0.64, 0.85 | 0.50 |
| Aggression | 0.11 | -0.20, 0.42 | 0.69 | -0.64, 0.85 | 0.49 |
| Boldness | 0.06 | -0.22, 0.34 | 0.43 | -0.67, 0.79 | 0.67 |
| Exploration | 0.04 | -0.25, 0.34 | 0.28 | -0.69, 0.78 | 0.78 |
| Sociality | 0.06 | -0.25, 0.37 | 0.39 | -0.68, 0.80 | 0.70 |
| Reptiles / Amphibians | | | | | |
| SMD | | | | | |
| QE=151.82 | P<0.0001 | | | | |
| F=1.29 | P=0.28 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.02 | 0.13 | 11 | | |

| | | | | | |
|--------------------------|-----------------|-------------------|----------------|----------------------------|----------------|
| Species Name | 0 | 0 | 10 | | |
| Obs | 0.06 | 0.24 | 95 | | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| Activity | -0.05 | -0.45, 0.36 | -0.23 | -0.72, 0.63 | 0.82 |
| Aggression | -0.07 | -0.32, 0.19 | -0.52 | -0.66, 0.53 | 0.60 |
| Boldness | 0.12 | -0.09, 0.33 | 1.11 | -0.46, 0.70 | 0.27 |
| Exploration | 0.25 | 0.05, 0.45 | 2.44 | -0.33, 0.83 | 0.02* |
| Sociality | -0.05 | -0.60, 0.50 | -0.18 | -0.82, 0.73 | 0.86 |
| <i>lnCVR</i> | | | | | |
| QE=73.79 | P=0.89 | | | | |
| F=1.31 | P=0.27 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.04 | 0.20 | 11 | | |
| Species Name | 0 | 0 | 10 | | |
| Obs | 0 | 0 | 95 | | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| Activity | -0.11 | -0.51, 0.29 | -0.53 | -0.67, 0.46 | 0.60 |
| Aggression | 0.33 | -0.05, 0.72 | 1.73 | -0.22, 0.89 | 0.09 |
| Boldness | 0.10 | -0.13, 0.33 | 0.83 | -0.36, 0.56 | 0.41 |
| Exploration | -0.10 | -0.35, 0.14 | -0.84 | -0.57, 0.36 | 0.40 |
| Sociality | -0.12 | -0.76, 0.52 | -0.38 | -0.87, 0.63 | 0.70 |

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Table S3. Subset meta-analysis models for each of the taxonomic groups /personality trait types where we could include sexual size dimorphism (SSD) as a moderator. There were not enough data to run models for the trait type Sociality, or for any trait for Reptiles/Amphibians. Intercept shows mean difference between males and females when SSD is 0 (no sexual size dimorphism), with the slope for SSD showing the mean difference when males become larger than females (positive SSD).

| | | | | |
|-------------------|-----------------|---------------------|----------------|----------------|
| Activity | | | | |
| Inverts | | | | |
| SMD | | | | |
| QE = 1069.50 | P<0.0001 | | | |
| F=0.67 | P=0.41 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 2.23 | 1.49 | 18 | |
| Species Name | 0 | 0.01 | 16 | |
| Obs | 0.15 | 0.39 | 165 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Intercept | 0.31 | -0.42, 1.04 | 0.83 | 0.38 |
| SSD | -0.66 | -2.26, 0.93 | -0.82 | 0.70 |
| lnCVR | | | | |
| QE = 475.98 | P = 0.12 | | | |
| F = 0.45 | P = 0.50 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.12 | 0.35 | 18 | |
| Species Name | 0 | 0 | 16 | |
| Obs | 0.05 | 0.23 | 165 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Intercept | -0.04 | -0.25, 0.17 | -0.36 | 0.72 |
| SSD | 0.27 | -0.53, 1.07 | 0.67 | 0.50 |
| Mammals | | | | |
| SMD | | | | |
| QE = 321.40 | P<0.0001 | | | |
| F=5.46 | P=0.02 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.10 | 0.32 | 14 | |
| Species Name | 2.13 | 1.46 | 12 | |
| Obs | 0.21 | 0.45 | 84 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Intercept | 0.44 | -1.74, 2.62 | 0.40 | 0.69 |
| SSD | -2.16 | -3.99, -0.32 | -2.34 | 0.02* |
| lnCVR | | | | |
| QE = 146.26 | P <0.0001 | | | |
| F = 5.46 | P = 0.02 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.03 | 0.32 | 14 | |
| Species Name | 2.13 | 1.46 | 12 | |
| Obs | 0.21 | 0.45 | 84 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Intercept | 0.05 | -0.15, 0.25 | 0.52 | 0.60 |
| SSD | 0.13 | -0.56, 0.81 | 0.36 | 0.72 |
| Aggression | | | | |
| Fish | | | | |
| SMD | | | | |
| QE=334.17 | P<0.0001 | | | |
| F=0.23 | P=0.63 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.02 | 0.14 | 16 | |
| Species Name | 0.33 | 0.58 | 13 | |

| | | | | |
|---------------------|-----------------|--------------------|----------------|----------------|
| Obs | 0.17 | 0.41 | 93 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Intercept | -0.16 | -0.96, 0.63 | -0.41 | 0.68 |
| SSD | 0.27 | -0.84, 1.37 | 0.48 | 0.63 |
| <i>lnCVR</i> | | | | |
| QE=68.27 | P=0.96 | | | |
| F=0.15 | P=0.70 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.02 | 0.15 | 16 | |
| Species Name | 0 | 0 | 13 | |
| Obs | 0 | 0 | 93 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Intercept | -0.12 | -0.23, 0.00 | -1.95 | 0.05* |
| SSD | -0.13 | -0.81, 0.55 | -0.39 | 0.70 |
| Mammals | | | | |
| <i>SMD</i> | | | | |
| QE=313.78 | P<0.0001 | | | |
| F=3.92 | P=0.05 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0 | 0 | 15 | |
| Species Name | 0.69 | 0.83 | 13 | |
| Obs | 0.14 | 0.38 | 85 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Intercept | -0.09 | -1.29, 1.10 | -0.16 | 0.88 |
| SSD | 1.36 | -0.01, 2.73 | 1.98 | 0.05* |
| <i>lnCVR</i> | | | | |
| QE=201.50 | P<0.0001 | | | |
| F=0.01 | P=0.94 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.18 | 0.42 | 15 | |
| Species Name | 0 | 0.01 | 13 | |
| Obs | 0.15 | 0.39 | 85 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Intercept | 0.09 | -0.21, 0.39 | 0.59 | 0.56 |
| SSD | -0.05 | -1.43, 1.33 | -0.07 | 0.94 |
| Boldness | | | | |
| Birds | | | | |
| <i>SMD</i> | | | | |
| QE=1592.83 | P<0.0001 | | | |
| F=0.15 | P=0.70 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 1.82 | 1.35 | 21 | |
| Species Name | 0 | 0.01 | 78 | |
| Obs | 0.11 | 0.33 | 233 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Intercept | -0.27 | -0.87, 0.33 | -0.88 | 0.38 |
| SSD | -0.23 | -1.45, 0.98 | -0.38 | 0.70 |
| <i>lnCVR</i> | | | | |
| QE=256.10 | P=0.12 | | | |
| F=0.59 | P=0.44 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0 | 0 | 21 | |
| Species Name | 0 | 0.06 | 78 | |
| Obs | 0 | 0 | 233 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Intercept | 0.03 | -0.04, 0.11 | 0.89 | 0.37 |
| SSD | 0.11 | -0.16, 0.37 | 0.77 | 0.44 |
| Fish | | | | |
| <i>SMD</i> | | | | |
| QE=614.58 | P<0.0001 | | | |
| F=1.07 | P=0.30 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |

| | | | | |
|---------------------|-----------------|----------------|----------------|----------------|
| Study ID | 0.02 | 0.13 | 23 | |
| Species Name | 0.03 | 0.16 | 12 | |
| Obs | 0.06 | 0.24 | 172 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Intercept | -0.04 | -0.33, 0.25 | -0.28 | 0.78 |
| SSD | 0.10 | -0.31, 0.52 | 0.49 | 0.63 |
| <i>lnCVR</i> | | | | |
| QE=307.62 | P<0.0001 | | | |
| F=0.24 | P=0.63 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.18 | 0.42 | 23 | |
| Species Name | 0 | 0.01 | 12 | |
| Obs | 0.15 | 0.39 | 172 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Intercept | 0.09 | -0.21, 0.39 | 0.59 | 0.56 |
| SSD | -0.05 | -1.43, 1.33 | -0.07 | 0.94 |
| Inverts | | | | |
| <i>SMD</i> | | | | |
| QE=923.09 | P<0.0001 | | | |
| F=0.46 | P=0.50 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.90 | 0.31 | 22 | |
| Species Name | 0 | 0 | 22 | |
| Obs | 0.32 | 0.56 | 161 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Intercept | 0.18 | -0.03, 0.38 | 1.68 | 0.09 |
| SSD | 0.28 | -0.54, 1.10 | 0.68 | 0.50 |
| <i>lnCVR</i> | | | | |
| QE=561.57 | P<0.0001 | | | |
| F=0.00 | P=0.95 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.03 | 0.16 | 22 | |
| Species Name | 0 | 0.01 | 22 | |
| Obs | 0.10 | 0.32 | 161 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Intercept | -0.04 | -0.16, 0.09 | -0.58 | 0.56 |
| SSD | 0.02 | -0.47, 0.51 | 0.07 | 0.95 |
| Mammals | | | | |
| <i>SMD</i> | | | | |
| QE=402.76 | P<0.0001 | | | |
| F=0.92 | P=0.34 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.02 | 0.16 | 26 | |
| Species Name | 0 | 0.05 | 26 | |
| Obs | 0.15 | 0.39 | 163 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Intercept | 0.09 | -0.09, 0.27 | 0.96 | 0.34 |
| SSD | -0.16 | -0.50, 0.17 | -0.96 | 0.34 |
| <i>lnCVR</i> | | | | |
| QE=175.27 | P<0.0001 | | | |
| F=0.88 | P=0.35 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0 | 0.03 | 26 | |
| Species Name | 0 | 0 | 26 | |
| Obs | 0.02 | 0.14 | 163 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Intercept | 0.07 | -0.03, 0.16 | 1.37 | 0.16 |
| SSD | 0.08 | -0.09, 0.25 | 0.94 | 0.35 |
| Exploration | | | | |
| Mammals | | | | |
| <i>SMD</i> | | | | |
| QE=658.46 | P<0.0001 | | | |

| | | | | |
|---------------------|-----------------|----------------|----------------|----------------|
| F=0.04 | P=0.85 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.05 | 0.22 | 19 | |
| Species Name | 0 | 0 | 16 | |
| Obs | 0.13 | 0.36 | 213 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Intercept | 0.00 | -0.18, 0.18 | -0.02 | 0.99 |
| SSD | -0.05 | -0.60, 0.50 | -0.19 | 0.85 |
| <i>lnCVR</i> | | | | |
| QE=361.16 | P<0.0001 | | | |
| F=0.27 | P=0.61 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.02 | 0.14 | 19 | |
| Species Name | 0.03 | 0.16 | 16 | |
| Obs | 0.03 | 0.18 | 213 | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Intercept | -0.06 | -0.36, 0.24 | -0.40 | 0.69 |
| SSD | 0.13 | -0.37, 0.64 | 0.52 | 0.61 |

Table S4. Sensitivity meta-regression models for each of the taxonomic groups with personality and precision both included as moderator terms. Including precision in our full trait models allows us to look for evidence of publication bias (as indicated when the slope for precision is significant). See Methods for calculation of precision.

| | | | | |
|--------------------------|-----------------|---------------------|----------------|----------------|
| Birds | | | | |
| <i>SMD</i> | | | | |
| QE=2670.88 | P<0.0001 | | | |
| F=3.20 | P=0.004 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.65 | 0.81 | 50 | |
| Species Name | 0 | 0 | 106 | |
| Obs | 0.14 | 0.38 | 483 | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Activity | -0.20 | -0.54, 0.14 | -1.16 | 0.25 |
| Aggression | -0.21 | -0.56, 0.14 | -1.19 | 0.23 |
| Boldness | -0.26 | -0.57, 0.05 | -1.16 | 0.11 |
| Exploration | 0.03 | -0.29, 0.35 | 0.18 | 0.86 |
| Sociality | -0.74 | -1.25, -0.24 | -2.88 | 0.004** |
| Precision | 0.01 | -0.02, 0.05 | 0.69 | 0.49 |
| <i>lnCVR</i> | | | | |
| QE=3683.35 | P<0.0001 | | | |
| F=0.99 | P=0.43 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.31 | 0.56 | 50 | |
| Species Name | 0 | 0 | 106 | |
| Obs | 0.39 | 0.62 | 483 | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Activity | 0.04 | -0.29, 0.36 | 0.21 | 0.83 |
| Aggression | -0.09 | -0.43, 0.26 | -0.48 | 0.63 |
| Boldness | -0.03 | -0.30, 0.25 | -0.18 | 0.86 |
| Exploration | -0.27 | -0.58, 0.04 | -1.73 | 0.08 |
| Sociality | 0.12 | -0.42, 0.66 | 0.44 | 0.66 |
| Precision | 0.00 | -0.03, 0.04 | 0.26 | 0.80 |
| Fish | | | | |
| <i>SMD</i> | | | | |
| QE=1342.38 | P<0.0001 | | | |
| F=1.56 | P=0.16 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.03 | 0.17 | 44 | |
| Species Name | 0.11 | 0.32 | 22 | |
| Obs | 0.13 | 0.37 | 493 | |

| | | | | |
|--------------------------|-----------------|---------------------|----------------|----------------|
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Activity | -0.23 | -0.79, 0.33 | -0.81 | 0.42 |
| Aggression | -0.11 | -0.63, 0.41 | -0.43 | 0.67 |
| Boldness | -0.22 | -0.76, 0.31 | -0.82 | 0.41 |
| Exploration | -0.11 | -0.64, 0.42 | -0.40 | 0.69 |
| Sociality | -0.47 | -1.03, 0.09 | -1.64 | 0.10 |
| Precision | 0.02 | -0.05, 0.08 | 0.55 | 0.58 |
| InCVR | | | | |
| QE=912.54 | P<0.0001 | | | |
| F=0.98 | P=0.44 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.01 | 0.10 | 44 | |
| Species Name | 0 | 0 | 22 | |
| Obs | 0.08 | 0.29 | 493 | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Activity | -0.07 | -0.26, 0.13 | -0.67 | 0.50 |
| Aggression | -0.15 | -0.32, 0.01 | -1.83 | 0.07 |
| Boldness | -0.06 | -0.22, 0.11 | -0.67 | 0.50 |
| Exploration | -0.06 | -0.22, 0.11 | -0.68 | 0.50 |
| Sociality | 0.03 | -0.19, 0.26 | 0.29 | 0.77 |
| Precision | 0.01 | -0.03, 0.05 | 0.46 | 0.65 |
| Inverts | | | | |
| SMD | | | | |
| QE=2656.83 | P<0.0001 | | | |
| F=2.58 | P=0.02 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.87 | 0.93 | 37 | |
| Species Name | 0 | 0 | 36 | |
| Obs | 0.32 | 0.57 | 422 | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Activity | 0.62 | 0.21, 1.03 | 2.95 | 0.003** |
| Aggression | 0.66 | -0.08, 1.39 | 1.76 | 0.08 |
| Boldness | 0.63 | 0.22, 1.05 | 2.99 | 0.003** |
| Exploration | 0.33 | -0.17, 0.82 | 1.30 | 0.19 |
| Sociality | 0.75 | -0.06, 1.56 | 1.83 | 0.07 |
| Precision | -0.08 | -0.13, -0.02 | -2.84 | 0.005** |
| InCVR | | | | |
| QE=1427.27 | P<0.0001 | | | |
| F=0.87 | P=0.52 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.04 | 0.19 | 37 | |
| Species Name | 0 | 0 | 36 | |
| Obs | 0.11 | 0.33 | 422 | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Activity | -0.07 | -0.23, 0.09 | -0.84 | 0.40 |
| Aggression | 0.16 | -0.13, 0.44 | 0.19 | 0.85 |
| Boldness | -0.05 | -0.21, 0.11 | -0.30 | 0.76 |
| Exploration | 0.06 | -0.16, 0.27 | 0.56 | 0.58 |
| Sociality | 0.26 | -0.17, 0.68 | 1.41 | 0.16 |
| Precision | 0.00 | -0.02, 0.03 | -0.03 | 0.97 |
| Mammals | | | | |
| SMD | | | | |
| QE=2147.01 | P<0.0001 | | | |
| F=1.36 | P=0.23 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.13 | 0.36 | 61 | |
| Species Name | 0.05 | 0.23 | 45 | |
| Obs | 0.15 | 0.39 | 674 | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Activity | -0.05 | -0.47, 0.37 | -0.24 | 0.81 |
| Aggression | 0.23 | -0.18, 0.64 | 1.10 | 0.27 |
| Boldness | 0.27 | -0.12, 0.65 | 1.37 | 0.17 |
| Exploration | 0.17 | -0.23, 0.56 | 0.82 | 0.41 |

| | | | | |
|------------------------------|-----------------|----------------|----------------|----------------|
| Sociality | 0.22 | -0.20, 0.63 | 1.02 | 0.31 |
| Precision | -0.03 | -0.09, 0.03 | -1.04 | 0.30 |
| <i>lnCVR</i> | | | | |
| QE=1039.19 | P<0.0001 | | | |
| F=0.26 | P=0.95 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.04 | 0.19 | 61 | |
| Species Name | 0.04 | 0.21 | 45 | |
| Obs | 0.04 | 0.19 | 674 | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Activity | 0.08 | -0.23, 0.39 | 0.48 | 0.63 |
| Aggression | 0.08 | -0.23, 0.39 | 0.51 | 0.61 |
| Boldness | 0.03 | -0.26, 0.32 | 0.21 | 0.83 |
| Exploration | 0.01 | -0.29, 0.31 | 0.09 | 0.93 |
| Sociality | 0.03 | -0.28, 0.34 | 0.20 | 0.84 |
| Precision | 0.01 | -0.02, 0.03 | 0.51 | 0.61 |
| Reptiles / Amphibians | | | | |
| <i>SMD</i> | | | | |
| QE=149.09 | P<0.0001 | | | |
| F=1.14 | P=0.35 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.03 | 0.16 | 11 | |
| Species Name | 0 | 0 | 10 | |
| Obs | 0.05 | 0.23 | 95 | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Activity | 0.66 | -0.43, 1.74 | 1.20 | 0.23 |
| Aggression | 0.80 | -0.51, 2.11 | 1.21 | 0.23 |
| Boldness | 0.78 | -0.19, 1.76 | 1.60 | 0.11 |
| Exploration | 0.87 | -0.06, 1.79 | 1.86 | 0.07 |
| Sociality | 0.60 | -0.45, 1.66 | 1.14 | 0.26 |
| Precision | -0.23 | -0.56, 0.10 | -1.40 | 0.17 |
| <i>lnCVR</i> | | | | |
| QE=73.63 | P=0.88 | | | |
| F=1.10 | P=0.37 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | |
| Study ID | 0.04 | 0.20 | 11 | |
| Species Name | 0 | 0 | 10 | |
| Obs | 0 | 0 | 95 | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> |
| Activity | -0.14 | -0.76, 0.49 | -0.43 | 0.67 |
| Aggression | 0.32 | -0.19, 0.82 | 1.24 | 0.22 |
| Boldness | 0.07 | -0.42, 0.56 | 0.28 | 0.78 |
| Exploration | -0.13 | -0.55, 0.30 | -0.59 | 0.56 |
| Sociality | -0.14 | -0.85, 0.56 | -0.40 | 0.69 |
| Precision | 0.01 | -0.12, 0.14 | 0.12 | 0.90 |

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Table S5. Primary and secondary keyword searches used for our literature search conducted on 11 December 2018. Keyword searches differed slightly to account for how operator terms are employed by each database. The searches were further refined by using relevant biological categories in ISI or SCOPUS.

| | <i>ISI Web of Science</i> | <i>SCOPUS</i> |
|---------------------------------------|--|--|
| <i>Primary keyword search terms</i> | (personalit* OR “behavioural syndrome*” OR “behavioral syndrome*” OR temperament) AND (sex*) NOT (man OR men OR woman OR women OR human) | personalit* OR “behavioural syndrome” OR “behavioral syndrome” OR temperament AND sex AND NOT man AND NOT woman AND NOT human |
| <i>Secondary keyword search terms</i> | animal* AND behav* AND (bold* OR shy* OR neoph* OR aggress* OR explor* OR hid*) AND “sex differences” NOT man NOT woman NOT human | animal* AND (bold* OR shy* OR neoph* OR aggress* OR explor* OR hid*) AND “sex differences” AND NOT man AND NOT woman AND NOT human |
| <i>Refined by categories</i> | zoology, ecology, biology, multidisciplinary sciences, evolutionary biology | agriculture & biology |

Table S6. Sensitivity contrast models for each of the taxonomic groups with score data type included as a moderator. These models compare score data to the rest of the dataset (intercept) to see if effect sizes calculated from scores are significantly different from our transformed (and normally-distributed) effect size dataset.

| | | | | | | |
|-----------------|-----------------|----------------|----------------|----------------|----------|--|
| Birds | | | | | | |
| SMD | | | | | | |
| Q=2723.54 | P<0.0001 | | | | | |
| F=0.25 | P=0.62 | | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | | |
| Study ID | 0.59 | 0.77 | 50 | | | |
| Species Name | 0 | 0.01 | 106 | | | |
| Obs | 0.16 | 0.40 | 483 | | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> | <i>k</i> | |
| Intercept | -0.12 | -0.352, 0.11 | -1.02 | 0.31 | 426 | |
| Scores | -0.06 | -0.30, 0.18 | -0.50 | 0.62 | 57 | |
| lnCVR | | | | | | |
| Q=3819.02 | P<0.0001 | | | | | |
| F=0.02 | P=0.88 | | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | | |
| Study ID | 0.01 | 0.12 | 50 | | | |
| Species Name | 0.36 | 0.6 | 106 | | | |
| Obs | 0.4 | 0.63 | 483 | | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> | <i>k</i> | |
| Intercept | -0.15 | -0.66, 0.36 | -0.57 | 0.57 | 426 | |
| Scores | 0.02 | -0.24, 0.28 | 0.16 | 0.88 | 57 | |
| Fish | | | | | | |
| SMD | | | | | | |
| Q=1380.98 | P<0.0001 | | | | | |
| F=0.62 | P=0.43 | | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | | |
| Study ID | 0.04 | 0.21 | 44 | | | |
| Species Name | 0.04 | 0.21 | 22 | | | |

| | | | | | |
|------------------------------|-----------------|---------------------|----------------|----------------|------------|
| Obs | 0.13 | 0.36 | 493 | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> | <i>k</i> |
| Intercept | -0.07 | -0.40, 0.27 | -0.4 | 0.69 | 435 |
| Scores | 0.08 | -0.12, 0.28 | 0.79 | 0.43 | 58 |
| <i>lnCVR</i> | | | | | |
| Q=915.16 | P<0.0001 | | | | |
| F=1.32 | P=0.25 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.01 | 0.07 | 44 | | |
| Species Name | 0 | 0 | 22 | | |
| Obs | 0.09 | 0.29 | 493 | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> | <i>k</i> |
| Intercept | -0.03 | -0.08, 0.03 | -0.98 | 0.33 | 435 |
| Scores | -0.08 | -0.22, 0.06 | -1.15 | 0.25 | 58 |
| Inverts | | | | | |
| <i>SMD</i> | | | | | |
| Q=2891.60 | P<0.0001 | | | | |
| F=4.45 | P=0.04 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.73 | 0.85 | 44 | | |
| Species Name | 0 | 0 | 41 | | |
| Obs | 0.27 | 0.52 | 483 | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> | <i>k</i> |
| Intercept | 0.3 | 0.02, 0.57 | 2.12 | 0.03* | 422 |
| Scores | -0.29 | -0.57, -0.02 | -2.11 | 0.04* | 61 |
| <i>lnCVR</i> | | | | | |
| Q=1536.77 | P<0.0001 | | | | |
| F=1.92 | P=0.17 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.04 | 0.2 | 44 | | |
| Species Name | 0 | 0 | 41 | | |
| Obs | 0.09 | 0.3 | 483 | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> | <i>k</i> |
| Intercept | 0.00 | -0.08, 0.08 | 0.00 | 0.999 | 422 |
| Scores | -0.11 | -0.26, 0.05 | -1.38 | 0.17 | 61 |
| Mammals | | | | | |
| <i>SMD</i> | | | | | |
| Q=2190.73 | P<0.0001 | | | | |
| F=2.64 | P=0.10 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.1 | 0.32 | 61 | | |
| Species Name | 0.07 | 0.26 | 45 | | |
| Obs | 0.16 | 0.39 | 674 | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> | <i>k</i> |
| Intercept | 0.13 | -0.21, 0.48 | 0.75 | 0.45 | 582 |
| Scores | -0.21 | -0.47, 0.04 | -1.62 | 0.10 | 92 |
| <i>lnCVR</i> | | | | | |
| Q=1074.89 | P<0.0001 | | | | |
| F=0.14 | P=0.71 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.03 | 0.18 | 61 | | |
| Species Name | 0.05 | 0.23 | 45 | | |
| Obs | 0.03 | 0.19 | 674 | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> | <i>k</i> |
| Intercept | 0.08 | -0.20, 0.36 | 0.55 | 0.58 | 582 |
| Scores | -0.03 | -0.22, 0.15 | -0.38 | 0.71 | 92 |
| Reptiles / Amphibians | | | | | |
| <i>SMD</i> | | | | | |
| Q=163.14 | P<0.0001 | | | | |
| F=0.17 | P=0.68 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |

| | | | | | |
|---------------------|-----------------|----------------|----------------|----------------|----------|
| Study ID | 0.03 | 0.19 | 11 | | |
| Species Name | 0 | 0.01 | 10 | | |
| Obs | 0.06 | 0.23 | 95 | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> | <i>k</i> |
| Intercept | 0.06 | -0.11, 0.23 | 0.70 | 0.49 | 92 |
| Scores | -0.42 | -0.44, 0.67 | 0.42 | 0.68 | 3 |
| <i>lnCVR</i> | | | | | |
| Q=77.56 | P=0.88 | | | | |
| F=0.23 | P=0.63 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0 | 0.01 | 11 | | |
| Species Name | 0 | 0.05 | 10 | | |
| Obs | 0 | 0.01 | 95 | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>p-value</i> | <i>k</i> |
| Intercept | 0.06 | -0.04, 0.16 | 1.15 | 0.26 | 92 |
| Scores | -0.09 | -0.46, 0.28 | -0.48 | 0.63 | 3 |

Table S7. Intercept-only meta-analysis models for each of the taxonomic groups with the inclusion of our **D** matrix ($r = 0.8$) as a random effect (replacing *obs*). These sensitivity models check whether correlations between personality traits measured on the same individuals, and on the same trait types in the same study, significantly change the interpretation of our models.

| | | | | | |
|---------------------|-----------------|----------------|----------------|----------------------------|----------------|
| Birds | | | | | |
| <i>SMD</i> | | | | | |
| Q=2804.93 | P<0.0001 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.45 | 0.67 | 50 | | |
| Species Name | 0 | 0.01 | 106 | | |
| Obs | 0.27 | 0.52 | 483 | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | -0.12 | -0.34, 0.97 | -1.09 | -1.80, 1.55 | 0.27 |
| <i>lnCVR</i> | | | | | |
| Q=3820.60 | P<0.0001 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0 | 0 | 50 | | |
| Species Name | 0 | 0 | 106 | | |
| Obs | 1.26 | 1.12 | 483 | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | -0.05 | -0.23, 0.13 | -0.54 | -2.26, 2.16 | 0.59 |
| Fish | | | | | |
| <i>SMD</i> | | | | | |
| Q=1385.84 | P<0.0001 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.01 | 0.1 | 44 | | |
| Species Name | 0.02 | 0.13 | 22 | | |
| Obs | 0.26 | 0.51 | 493 | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | 0.05 | -0.19, 0.28 | 0.41 | -1.02, 1.12 | 0.68 |
| <i>lnCVR</i> | | | | | |
| Q=924.06 | P<0.0001 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0 | 0 | 44 | | |
| Species Name | 0 | 0 | 22 | | |
| Obs | 0.09 | 0.31 | 493 | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | -0.03 | -0.09, 0.03 | -0.98 | -0.64, 0.57 | 0.33 |
| Inverts | | | | | |

| | | | | | |
|------------------------------|-----------------|----------------|----------------|----------------------------|----------------|
| SMD | | | | | |
| Q=2678.23 | | P<0.0001 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.9 | 0.95 | 37 | | |
| Species Name | 0 | 0 | 36 | | |
| Obs | 0.77 | 0.88 | 422 | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | 0.31 | -0.05, 0.67 | 1.69 | -2.26, 2.87 | 0.09 |
| lnCVR | | | | | |
| Q=1459.70 | | P<0.0001 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.01 | 0.11 | 37 | | |
| Species Name | 0.01 | 0.08 | 36 | | |
| Obs | 0.24 | 0.49 | 422 | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | 0.00 | -0.13, 0.13 | -0.01 | -1.00, 1.00 | 0.99 |
| Mammals | | | | | |
| SMD | | | | | |
| Q=2218.15 | | P<0.0001 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.02 | 0.15 | 61 | | |
| Species Name | 0.08 | 0.29 | 45 | | |
| Obs | 0.32 | 0.56 | 674 | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | 0.07 | -0.30, 0.43 | 0.36 | -1.26, 1.39 | 0.72 |
| lnCVR | | | | | |
| Q=1074.96 | | P<0.0001 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.02 | 0.15 | 61 | | |
| Species Name | 0.12 | 0.13 | 45 | | |
| Obs | 0.04 | 0.21 | 674 | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | 0.05 | -0.12, 0.23 | 0.59 | -0.54, 0.65 | 0.55 |
| Reptiles / Amphibians | | | | | |
| SMD | | | | | |
| Q=163.37 | | P<0.0001 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.03 | 0.18 | 11 | | |
| Species Name | 0 | 0.01 | 10 | | |
| Obs | 0.05 | 0.23 | 95 | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | 0.07 | -0.09, 0.23 | 0.84 | -0.54, 0.67 | 0.40 |
| lnCVR | | | | | |
| Q=77.72 | | P=0.89 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0 | 0 | 11 | | |
| Species Name | 0 | 0.03 | 10 | | |
| Obs | 0.01 | 0.11 | 95 | | |
| <i>Model</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| | 0.05 | -0.05, 0.14 | 0.98 | -0.20, 0.30 | 0.33 |

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Table S8. Multi-level meta-regression models for each of the taxonomic groups with personality trait type as a moderator and the inclusion of our D matrix ($r = 0.8$) as a random effect (reported here as *obs*). These sensitivity models check whether correlations between personality traits measured on the same individuals, or on the same trait types within the same study, significantly change the interpretation of our models.

| | | | | | |
|-------------------|----------|--------------|---------|---------------------|---------|
| Birds | | | | | |
| SMD | | | | | |
| QE=2670.89 | P<0.0001 | | | | |
| F=2.19 | P=0.05 | | | | |
| Variance | Estimate | SQRT | n | | |
| Study ID | 0.52 | 0.72 | 50 | | |
| Species Name | 0 | 0 | 106 | | |
| Obs | 0.23 | 0.48 | 483 | | |
| Personality Trait | Estimate | 95% CIs | t-score | Prediction Interval | p-value |
| Activity | -0.11 | -0.47, 0.25 | -0.60 | -1.85, 1.63 | 0.55 |
| Aggression | -0.05 | -0.39, 0.30 | -0.26 | -1.78, 1.69 | 0.79 |
| Boldness | -0.20 | -0.45, 0.06 | -1.51 | -1.92, 1.53 | 0.13 |
| Exploration | 0.03 | -0.24, 0.30 | 0.24 | -1.69, 1.76 | 0.81 |
| Sociality | -0.60 | -1.18, -0.02 | -2.02 | -2.40, 1.20 | 0.04* |
| lnCVR | | | | | |
| QE=3711.80 | P<0.0001 | | | | |
| F=0.20 | P=0.96 | | | | |
| Variance | Estimate | SQRT | n | | |
| Study ID | 0 | 0 | 50 | | |
| Species Name | 0 | 0 | 106 | | |
| Obs | 1.27 | 1.13 | 483 | | |
| Personality Trait | Estimate | 95% CIs | t-score | Prediction Interval | p-value |
| Activity | -0.24 | -0.73, 0.26 | -0.94 | -2.51, 2.04 | 0.35 |
| Aggression | -0.01 | -0.47, 0.45 | -0.04 | -2.27, 2.26 | 0.97 |
| Boldness | -0.03 | -0.27, 0.21 | -0.24 | -2.26, 2.20 | 0.81 |
| Exploration | -0.04 | -0.34, 0.26 | -0.25 | -2.28, 2.20 | 0.80 |
| Sociality | 0.08 | -0.63, 0.79 | 0.22 | -2.25, 2.41 | 0.82 |
| Fish | | | | | |
| SMD | | | | | |
| QE=1347.79 | P<0.0001 | | | | |
| F=0.59 | P=0.71 | | | | |
| Variance | Estimate | SQRT | n | | |
| Study ID | 0 | 0 | 44 | | |
| Species Name | 0.06 | 0.24 | 22 | | |
| Obs | 0.26 | 0.51 | 493 | | |
| Personality Trait | Estimate | 95% CIs | t-score | Prediction Interval | p-value |
| Activity | 0.07 | -0.36, 0.50 | 0.31 | -1.12, 1.26 | 0.75 |
| Aggression | 0.05 | -0.35, 0.45 | 0.25 | -1.12, 1.23 | 0.80 |
| Boldness | -0.02 | -0.42, 0.37 | -0.12 | -1.20, 1.15 | 0.90 |
| Exploration | -0.01 | -0.43, 0.42 | -0.04 | -1.19, 1.17 | 0.97 |
| Sociality | -0.21 | -0.69, 0.26 | -0.87 | -1.41, 0.99 | 0.38 |
| lnCVR | | | | | |
| QE=915.16 | P<0.0001 | | | | |
| F=1.04 | P=0.39 | | | | |
| Variance | Estimate | SQRT | n | | |
| Study ID | 0 | 0 | 44 | | |
| Species Name | 0 | 0 | 22 | | |
| Obs | 0.1 | 0.31 | 493 | | |
| Personality Trait | Estimate | 95% CIs | t-score | Prediction Interval | p-value |
| Activity | -0.06 | -0.22, 0.11 | -0.71 | -0.69, 0.57 | 0.48 |
| Aggression | -0.13 | -0.26, 0.00 | -1.95 | -0.76, 0.50 | 0.05* |
| Boldness | 0.02 | -0.08, 0.12 | 0.46 | -0.60, 0.64 | 0.65 |
| Exploration | -0.04 | -0.19, 0.11 | -0.57 | -0.67, 0.59 | 0.57 |
| Sociality | 0.06 | -0.16, 0.28 | 0.55 | -0.59, 0.71 | 0.58 |
| Inverts | | | | | |

| | | | | | |
|------------------------------|-----------------|-------------------|----------------|----------------------------|----------------|
| SMD | | | | | |
| QE=2657.20 | | P<0.0001 | | | |
| F=1.44 | | P=0.21 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.88 | 0.94 | 37 | | |
| Species Name | 0 | 0 | 36 | | |
| Obs | 0.78 | 0.89 | 422 | | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| Activity | 0.56 | 0.12, 1.00 | 2.50 | -2.01, 3.13 | 0.01* |
| Aggression | 0.22 | -0.71, 1.15 | 0.46 | -2.48, 2.92 | 0.65 |
| Boldness | 0.17 | -0.25, 0.59 | 0.79 | -2.40, 2.74 | 0.43 |
| Exploration | 0.10 | -0.52, 0.72 | 0.31 | -2.51, 2.71 | 0.76 |
| Sociality | 0.35 | -0.60, 1.31 | 0.72 | -2.35, 3.06 | 0.47 |
| lnCVR | | | | | |
| QE=1427.81 | | P<0.0001 | | | |
| F=0.37 | | P=0.87 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.01 | 0.1 | 37 | | |
| Species Name | 0.01 | 0.08 | 36 | | |
| Obs | 0.24 | 0.49 | 422 | | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| Activity | -0.04 | -0.21, 0.13 | -0.47 | -1.06, 0.97 | 0.64 |
| Aggression | 0.16 | -0.22, 0.54 | 0.85 | -0.91, 1.23 | 0.40 |
| Boldness | -0.01 | -0.18, 0.16 | -0.14 | -1.03, 1.00 | 0.89 |
| Exploration | 0.07 | -0.21, 0.35 | 0.47 | -0.97, 1.11 | 0.64 |
| Sociality | 0.23 | -0.33, 0.79 | 0.79 | -0.92, 1.37 | 0.43 |
| Mammals | | | | | |
| SMD | | | | | |
| QE=2158.51 | | P<0.0001 | | | |
| F=1.01 | | P=0.41 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.03 | 0.16 | 61 | | |
| Species Name | 0.06 | 0.24 | 45 | | |
| Obs | 0.32 | 0.57 | 674 | | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| Activity | -0.18 | -0.59, 0.22 | -0.90 | -1.50, 1.13 | 0.37 |
| Aggression | 0.16 | -0.23, 0.56 | 0.80 | -1.15, 1.47 | 0.42 |
| Boldness | 0.08 | -0.25, 0.41 | 0.48 | -1.22, 1.38 | 0.63 |
| Exploration | 0.01 | -0.35, 0.37 | 0.06 | -1.29, 1.31 | 0.95 |
| Sociality | 0.18 | -0.22, 0.58 | 0.87 | -1.14, 1.49 | 0.38 |
| lnCVR | | | | | |
| QE=1044.60 | | P<0.0001 | | | |
| F=0.64 | | P=0.67 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.02 | 0.15 | 61 | | |
| Species Name | 0.01 | 0.1 | 45 | | |
| Obs | 0.05 | 0.22 | 674 | | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| Activity | 0.11 | -0.09, 0.31 | 1.09 | -0.48, 0.70 | 0.28 |
| Aggression | 0.08 | -0.12, 0.28 | 0.76 | -0.51, 0.67 | 0.45 |
| Boldness | 0.06 | -0.10, 0.21 | 0.71 | -0.52, 0.63 | 0.48 |
| Exploration | 0.00 | -0.17, 0.18 | 0.03 | -0.58, 0.58 | 0.98 |
| Sociality | -0.03 | -0.24, 0.18 | -0.29 | -0.62, 0.56 | 0.77 |
| Reptiles / Amphibians | | | | | |
| SMD | | | | | |
| QE=151.82 | | P<0.0001 | | | |
| F=1.20 | | P=0.32 | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.02 | 0.13 | 11 | | |
| Species Name | 0 | 0 | 10 | | |
| Obs | 0.06 | 0.25 | 95 | | |

| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
|--------------------------|-----------------|-------------------|----------------|----------------------------|----------------|
| Activity | -0.07 | -0.50, 0.36 | -0.34 | -0.77, 0.62 | 0.73 |
| Aggression | -0.08 | -0.34, 0.19 | -0.57 | -0.69, 0.53 | 0.57 |
| Boldness | 0.12 | -0.12, 0.36 | 0.97 | -0.48, 0.72 | 0.33 |
| Exploration | 0.26 | 0.04, 0.49 | 2.32 | -0.33, 0.86 | 0.02* |
| Sociality | -0.04 | -0.62, 0.53 | -0.15 | -0.84, 0.75 | 0.88 |
| <i>lnCVR</i> | | | | | |
| QE=73.79 | P=0.89 | | | | |
| F=1.19 | P=0.32 | | | | |
| <i>Variance</i> | <i>Estimate</i> | <i>SQRT</i> | <i>n</i> | | |
| Study ID | 0.04 | 0.19 | 11 | | |
| Species Name | 0 | 0 | 10 | | |
| Obs | 0 | 0 | 95 | | |
| <i>Personality Trait</i> | <i>Estimate</i> | <i>95% CIs</i> | <i>t-score</i> | <i>Prediction Interval</i> | <i>p-value</i> |
| Activity | -0.11 | -0.52, 0.30 | -0.53 | -0.71, 0.49 | 0.60 |
| Aggression | 0.32 | -0.05, 0.70 | 1.71 | -0.25, 0.90 | 0.09 |
| Boldness | 0.10 | -0.14, 0.33 | 0.80 | -0.40, 0.59 | 0.42 |
| Exploration | -0.10 | -0.35, 0.15 | -0.81 | -0.60, 0.40 | 0.42 |
| Sociality | -0.11 | -0.76, 0.54 | -0.33 | -0.89, 0.67 | 0.74 |

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Table S9. Studies included in our final dataset and used in our meta-analysis (also included in reference list, refs 71-271 in bold).

| Study ID | Year Published | Article Title | Authors | Reference |
|----------|----------------|--|---|-----------|
| P001 | 2012 | The Social Behavior of Brown Spider Monkeys (<i>Ateles hybridus</i>) in a Fragmented Forest in Colombia | Abondano, L.A.; Link, A. | (71) |
| P002 | 2018 | Personality links with lifespan in chimpanzees | Altschul, D.M.; Hopkins, W.D.; Herrelko, E.S.; Inoue-Murayama, M.; Matsuzawa, T.; King, J.E.; Ross, S.R.; Weiss, A. | (72) |
| P003 | 2014 | Selective aggressiveness in European free-tailed bats (<i>Tadarida teniotis</i>): Influence of familiarity, age and sex | Ancillotto, L.; Russo, D. | (73) |
| P004 | 2018 | Innovation as part of a wider behavioural syndrome in the guppy: The effect of sex and body size | Berdal, M.A.; Rosenqvist, G.; Wright, J. | (74) |
| P006 | 2009 | Sex-dependent use of information on conspecific feeding activities in an amphibian urodelian | Aragon, P. | (75) |
| P008 | 2011 | Variation in aggressive behaviour in the poeciliid fish <i>Brachyrhaphis episcopi</i> : Population and sex differences | Archard, G. A.; Braithwaite, V.A. | (76) |
| P009 | 2013 | Disassortative mating for boldness decreases reproductive success in the guppy | Ariyomo, T.O.; Watt, P.J. | (77) |
| P010 | 2013 | Aggression and sex differences in lateralization in the zebrafish | Ariyomo, T.O.; Watt, P.J. | (78) |
| P011 | 2015 | Effect of hunger level and time of day on boldness and aggression in the zebrafish <i>Danio rerio</i> | Ariyomo, T.O.; Watt, P.J. | (79) |
| P013 | 2018 | Repeatability and reliability of exploratory behavior in proactive and reactive zebrafish, <i>Danio rerio</i> | Baker, M.R.; Goodman, A.C.; Santo, J.B.; Wong, R.Y. | (80) |
| P014 | 2015 | Juvenile social relationships reflect adult patterns of behavior in wild geladas | Barale, C.L.; Rubenstein, D.I.; Beehner, J.C. | (81) |
| P015 | 2016 | Phenotype Matching and Early Social Conditions Affect Shoaling and Exploration Decisions | Barbosa, M.; Camacho-Cervantes, M.; Ojanguren, A.F. | (82) |
| P016 | 2016 | Predator-prey interactions mediated by prey personality and predator hunting mode | Belgrad, B.A.; Griffen, B.D. | (83) |
| P017 | 2016 | Sexually antagonistic selection on genetic variation underlying both male and female same-sex sexual behavior | Berger, D.; You, T.; Minano, M.R.; Grieshop, K.; Lind, M.I.; Arnqvist, G.; Maklakov, A.A. | (84) |
| P018 | 2012 | Experimental evidence that adult antipredator behaviour is heritable and not influenced by behavioural copying in a wild bird | Bize, P.; Diaz, C.; Lindström, J. | (85) |
| P019 | 2017 | Boldness towards novel objects predicts predator inspection in wild vervet monkeys | Blaszczyk, M.B. | (86) |
| P020 | 2013 | Cannibalism as an interacting phenotype: Precannibalistic aggression is influenced by social partners in the endangered Socorro Isopod (<i>Thermosphaeroma thermophilum</i>) | Bleakley, B.H.; Welter, S.M.; McCauley-Cole, K.; Shuster, S.M.; Moore, A.J. | (87) |
| P021 | 2005 | Sexually dimorphic patterns of space use throughout ontogeny in the spotted hyena (<i>Crocuta crocuta</i>) | Boydston, E.E.; Kapheim, K.M.; Van Horn, R.C.; Smale, L.; Holekamp, K.E. | (88) |

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|------|------|---|--|-------|
| P022 | 2014 | Individual variation in dispersal associated behavioral traits of the invasive Chinese mitten crab (<i>Eriocheir sinensis</i> , H. Milne Edwards, 1854) during initial invasion of Lake Vänern, Sweden | Brodin, T.; Drotz, M.K. | (89) |
| P023 | 2007 | Heritable and experiential effects on boldness in a tropical poeciliid | Brown, C.; Burgess, F.; Braithwaite, V.A. | (90) |
| P024 | 1999 | Differences in measures of exploration and fear in MHC-congenic C57BL/6J and B6-H-2K mice | Brown, R.E.; Corey, S.C.; Moore, A.K. | (91) |
| P025 | 1978 | SEX-DIFFERENCES, DOMINANCE, AND PERSONALITY IN CHIMPANZEE | Buirski, P.; Plutchik, R.; Kellerman, H. | (92) |
| P026 | 2015 | Similar nest defence strategies within pairs increase reproductive success in the eastern bluebird, <i>Sialia sialis</i> | Burtka, J.L.; Grindstaff, J.L. | (93) |
| P027 | 2016 | Into the wild: Developing field tests to examine the link between elasmobranch personality and laterality | Byrnes, E.E.; Pouca, C.V.; Chambers, S.L.; Brown, C. | (94) |
| P028 | 2011 | Personality traits and the effects of DHA supplementation in the budgerigar (<i>Melopsittacus undulatus</i>) | Callicrate, T.E.; Siewerd, F.; Koutsos, E.; Estevez, I. | (95) |
| P029 | 2013 | Individual and spatio-temporal variations in the home range behaviour of a long-lived, territorial species | Campioni, L.; Delgado, M.M.; Lourenço, R.; Bastianelli, G.; Fernandez, N.; Penteriani, V. | (96) |
| P030 | 2017 | Mate similarity in foraging Kerguelen shags: A combined bio-logging and stable isotope investigation | Camprasse, E.C.M.; Cherel, Y.; Arnould, J.P.Y.; Hoskins, A.J.; Bustamante, P.; Bost, C.-A. | (97) |
| P031 | 2015 | Aggression and sociality: conflicting or complementary traits of a successful invader? | Capelle, P.M.; McCallum, E.S.; Balshine, S. | (98) |
| P032 | 2005 | Personalities in great tits, <i>Parus major</i> : Stability and consistency | Carere, C.; Drent, P.J.; Privitera, L.; Koolhaas, J.M.; Groothuis, T.G.G. | (99) |
| P033 | 2013 | Temperature-Specific Competition between Invasive Mosquitofish and an Endangered Cyprinodontid Fish | Carmona-Catot, G.; Magellan, K.; Carcêa-Berthou, E. | (100) |
| P034 | 2017 | Individual and sex differences in high and low responder phenotypes | Carreira, M.B.; Cossio, R.; Britton, G.B. | (101) |
| P035 | 2010 | Individual consistency in flight initiation distances in burrowing owls: A new hypothesis on disturbance-induced habitat selection | Carrete, M.; Tella, J.L. | (102) |
| P036 | 2013 | High individual consistency in fear of humans throughout the adult lifespan of rural and urban burrowing owls | Carrete, M.; Tella, J.L. | (103) |
| P037 | 2011 | Behavioral responses to physical vs. social novelty in male and female laboratory rats | Cavigelli, S.A.; Michael, K.C.; West, S.G.; Klein, L.C. | (104) |
| P039 | 2013 | Sex and the Syndrome: Individual and Population Consistency in Behaviour in Rock Pool Prawn <i>Palaemon elegans</i> | Chapman, B.B.; Hegg, A.; Ljungberg, P. | (105) |
| P040 | 2018 | Personality differentially affects individual mate choice decisions in female and male Western mosquitofish (<i>Gambusia affinis</i>) | Chen, B.-J.; Liu, K.; Zhou, L.-J.; Gomes-Silva, G.; Sommer-Trembo, C.; Plath, M. | (106) |
| P041 | 2015 | A strong genetic correlation underlying a behavioural syndrome disappears during development because of genotype-age interactions | Class, B.; Brommer, J.E. | (107) |

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|------|------|--|--|-------|
| P042 | 2015 | Long-Term Provision of Environmental Resources Alters Behavior but not Physiology or Neuroanatomy of Male and Female BALB/c and C57BL/6 Mice | Clipperton-Allen, A.E.; Ingrao, J.C.; Ruggiero, L.; Batista, L.; Ovari, J.; Hammermueller, J.; Armstrong, J.N.; Bienzle, D.; Choleris, E.; Turner, P.V. | (108) |
| P043 | 2002 | Counter aggression and reconciliation in Assamese macaques (<i>Macaca assamensis</i>) | Cooper, M.A.; Bernstein, I.S. | (109) |
| P045 | 2017 | Effects of captivity on house mice behaviour in a novel environment: Implications for conservation practices | Courtney Jones, S.K.; Munn, A.J.; Byrne, P.G. | (110) |
| P047 | 2011 | Boldness predicts social status in zebrafish (<i>Danio rerio</i>) | Dahlbom, S.J.; Lagman, D.; Lundstedt-Enkel, K.; Sundström, L.F.; Winberg, S. | (111) |
| P048 | 2012 | Are personality differences in a small iteroparous mammal maintained by a life-history trade-off? | Dammhahn, M. | (112) |
| P049 | 2014 | Shaping the antipredator strategy: Flexibility, consistency, and behavioral correlations under varying predation threat | David, M.; Salignon, M.; Perrot-Minnot, M.-J. | (113) |
| P050 | 2016 | Integrating the pace-of-life syndrome across species, sexes and individuals: Covariation of life history and personality under pesticide exposure | Debecker, S.; Sanmartên-Villar, I.; de Guinea-Luengo, M.; Cordero-Rivera, A.; Stoks, R. | (114) |
| P051 | 2015 | Short- and long-term repeatability of docility in the roe deer: Sex and age matter | Debeffe, L.; Lemaître, J.F.; Bergvall, U.A.; Hewison, A.J.M.; Gaillard, J.M.; Morellet, N.; Goulard, M.; Goulard, M.; Monestier, C.; David, M.; Verheyden-Tixier, H.; Jäderberg, L.; Vanpé, C.; Kjellander, P. | (115) |
| P052 | 2014 | The link between behavioural type and natal dispersal propensity reveals a dispersal syndrome in a large herbivore | Debeffe, L.; Morellet, N.; Bonnot, N.; Gaillard, J.M.; Cargnelutti, B.; Verheyden-Tixier, H.; Vanpé, C.; Coulon, A.; Clobert, J.; Bon, R.; Hewison, A.J.M. | (116) |
| P053 | 2016 | Exploration in a dispersal task: Effects of early experience and correlation with other behaviors in prairie voles (<i>Microtus ochrogaster</i>) | del Razo, R.A.; Bales, K.L. | (117) |
| P055 | 2003 | Natal dispersal and personalities in great tits (<i>Parus major</i>) | Dingemanse, N.J.; Both, C.; Van Noordwijk, A.J.; Rutten, A.L.; Drent, P.J. | (118) |
| P056 | 2009 | Evolution of genetic integration between dispersal and colonization ability in a bird | Duckworth, R.A.; Kruuk, L.E.B. | (119) |
| P057 | 2017 | Personality types in budgerigars, <i>Melopsittacus undulatus</i> | Duggan, M.R.; Lee-Soety, J.Y.; Anderson, M.J. | (120) |
| P058 | 2011 | Personality and parasites: Sex-dependent associations between avian malaria infection and multiple behavioural traits | Dunn, J.C.; Cole, E.F.; Quinn, J.L. | (121) |
| P060 | 2009 | Habituation potential of yellow-eyed penguins depends on sex, character and previous experience with humans | Ellenberg, U.; Mattern, T.; Seddon, P.J. | (122) |
| P061 | 2018 | Sex-specific cognitive-behavioural profiles emerging from individual variation in numerosity discrimination in <i>Gambusia affinis</i> | Etheredge, R.I.; Avenas, C.; Armstrong, M.J.; Cummings, M.E. | (123) |

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|------|------|--|--|-------|
| P065 | 1990 | Temperament in a fish: a longitudinal study of the development of individual differences in aggression and social rank in the Midas Cichlid | Francis, R.C. | (124) |
| P066 | 1999 | Inter-individual distances during open-field tests in Japanese quail (<i>Coturnix japonica</i>) selected for high or low levels of social reinstatement behaviour | François, N.; Mills, A.D.; Faure, J.M. | (125) |
| P067 | 1981 | Sexual dimorphism in responses to unfamiliar intruders in the tamarin, <i>Saguinus oedipus</i> | French, J.A.; Snowdon, C.T. | (126) |
| P068 | 2014 | A sex-specific behavioral syndrome in a wild passerine | Fresneau, N.; Klueen, E.; Brommer, J.E. | (127) |
| P069 | 2016 | Acoustic signalling reflects personality in a social mammal | Friel, M.; Kunc, H.P.; Griffin, K.; Asher, L.; Collins, L.M. | (128) |
| P070 | 2015 | Consistent individual differences in haemolymph density reflect risk propensity in a marine invertebrate | Furtbauer, I. | (129) |
| P071 | 2010 | Behavioural syndromes in Steller's jays: The role of time frames in the assessment of behavioural traits | Gabriel, P.O.; Black, J.M. | (130) |
| P072 | 2018 | Physiological and behavioral responses of house sparrows to repeated stressors | Gormally, B.M.G.; Wright-Lichter, J.; Reed, J.M.; Romero, L.M. | (131) |
| P073 | 2014 | Turning shy on a winter's day: Effects of season on personality and stress response in <i>Microtus arvalis</i> | Gracceva, G.; Herde, A.; Groothuis, T.G.G.; Koolhaas, J.M.; Palme, R.; Eccard, J.A. | (132) |
| P074 | 2017 | Is the behavioural divergence between range-core and range-edge populations of cane toads (<i>Rhinella marina</i>) due to evolutionary change or developmental plasticity? | Gruber, J.; Brown, G.; Whiting, M.J.; Shine, R. | (133) |
| P075 | 2018 | Behavioural divergence during biological invasions: A study of cane toads (<i>Rhinella marina</i>) from contrasting environments in Hawai'i | Gruber, J.; Brown, G.; Whiting, M.J.; Shine, R. | (134) |
| P076 | 2018 | Variation in personality traits across a metal pollution gradient in a free-living songbird | Grunst, A.S.; Grunst, M.L.; Thys, B.; Raap, T.; Daem, N.; Pinxten, R.; Eens, M. | (135) |
| P077 | 2018 | Are the big and beautiful less bold? Differences in avian fearfulness between the sexes in relation to body size and colour | Guay, P.-J.; Leppitt, R.; Weston, M.A.; Yeager, T.R.; van Dongen, W.F.D.; Symonds, M.R.E. | (136) |
| P078 | 2014 | The ontogeny of personality in the wild guinea pig | Guenther, A.; Finkemeier, M.-A.; Trillmich, F. | (137) |
| P083 | 2015 | Intimidating courtship and sex differences in predation risk lead to sex-specific behavioural syndromes | Han, C.S.; Jablonski, P.G.; Brooks, R.C. | (138) |
| P084 | 2015 | Sex-specific dispersal responses to inbreeding and kinship | Hardouin, L.A.; Legagneux, P.; Hingrat, Y.; Robert, A. | (139) |
| P085 | 2011 | Changes in behavioural trait integration following rapid ecotype divergence in an aquatic isopod | Harris, S.; Eroukhmanoff, F.; Green, K.K.; Svensson, E.I.; Pettersson, L.B. | (140) |
| P086 | 2010 | Picking personalities apart: Estimating the influence of predation, sex and body size on boldness in the guppy <i>Poecilia reticulata</i> | Harris, S.; Ramnarine, I.W.; Smith, H.G.; Pettersson, L.B. | (141) |
| P087 | 2010 | Individuality in the predator defense behaviour of the crab <i>Heterozius rotundifrons</i> | Hazlett, B.A.; Bach, C.E. | (142) |
| P088 | 2018 | Gender difference in unconditioned and conditioned predator fear responses in Smith's zokors (<i>Eospalax smithii</i>) | Hegab, I.M.; Qian, Z.; Pu, Q.; Wang, Z.; Yukun, K.; Cai, Z.; Guo, H.; Wang, H.; Ji, W.; Hanafy, A.M.; Su, J. | (143) |

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| P089 | 2016 | Predicting multifarious behavioural divergence in the wild | Heinen-Kay, J.L.; Schmidt, D.A.; Stafford, A.T.; Costa, M.T.; Peterson, M.N.; Kern, E.M.A.; Langerhans, R.B. | (144) |
| P091 | 2005 | Quantitative genetics of natural variation of behavior in <i>Drosophila melanogaster</i> : The possible role of the social environment on creating persistent patterns of group activity | Higgins, L.A.; Jones, K.M.; Wayne, M.L. | (145) |
| P092 | 2016 | Population differentiation and behavioural association of the two 'personality' genes DRD4 and SERT in dunnocks (<i>Prunella modularis</i>) | Holtmann, B.; Grosser, S.; Lagisz, M.; Johnson, S.L.; Santos, E.S.A.; Lara, C.E.; Robertson, B.C.; Nakagawa, S. | (146) |
| P093 | 2017 | Personality-matching habitat choice, rather than behavioural plasticity, is a likely driver of a phenotype-environment covariance | Holtmann, B.; Santos, E.S.A.; Lara, C.E.; Nakagawa, S. | (147) |
| P095 | 2016 | Behavioral, morphometric, and gene expression effects in adult zebrafish (<i>Danio rerio</i>) embryonically exposed to PFOA, PFOS, and PFNA | Jantzen, C.E.; Annunziato, K.M.; Cooper, K.R. | (148) |
| P096 | 2012 | Spatial navigation strategies in <i>Peromyscus</i> : a comparative study | Jašarević, E.; Williams, S.A.; Roberts, R. M.; Geary, D.C.; Rosenfeld, C.S. | (149) |
| P097 | 2015 | Sex differences in risk-taking and associative learning in rats | Jolles, J.W.; Boogert, N.J.; van den Bos, R. | (150) |
| P098 | 2018 | Behavioral variation post-invasion: Resemblance in some, but not all, behavioral patterns among invasive and native praying mantids | Jones, C.; DiRienzo, N. | (151) |
| P099 | 2018 | Urbanisation and sex affect the consistency of butterfly personality across metamorphosis | Kaiser, A.; Merckx, T.; Van Dyck, H. | (152) |
| P100 | 2017 | Adult wheel access interaction with activity and boldness personality in Siberian dwarf hamsters (<i>Phodopus sungorus</i>) | Kanda, L.L.; Abdulhay, A.; Erickson, C. | (153) |
| P101 | 2007 | The influence of sex, line, and fight experience on aggressiveness of the Siamese fighting fish in intrasexual competition | Karino, K.; Someya, C. | (154) |
| P102 | 2018 | Consistently bolder turtles maintain higher body temperatures in the field but may experience greater predation risk | Kashon, E.A.F.; Carlson, B.E. | (155) |
| P104 | 2016 | Unsociable juvenile male three-spined sticklebacks grow more attractive | Kim, S.-Y.; Velando, A. | (156) |
| P105 | 2001 | Spatial learning and memory in the blind mole-rat in comparison with the laboratory rat and Levant vole | Kimchi, T.; Terkel, J. | (157) |
| P106 | 2013 | Sex-differences and temporal consistency in stickleback fish boldness | King, A.J.; Fürtbauer, I.; Mamuneas, D.; James, C.; Manica, A. | (158) |
| P111 | 2014 | Artificial selection on relative brain size reveals a positive genetic correlation between brain size and proactive personality in the guppy | Kotrschal, A.; Lievens, E.J.; Dahlbom, J.; Bundsen, A.; Semenova, S.; Sundvik, M.; Maklakov, A.A.; Winberg, S.; Panula, P.; Kolm, N. | (159) |
| P112 | 2017 | Different patterns of behavioral variation across and within species of spiders with differing degrees of urbanization | Kralj-Fišer, S.; Hebets, E.A.; Kuntner, M. | (160) |
| P113 | 2014 | Sex-specific associations between nest defence, exploration and breathing rate in breeding pied flycatchers | Krams, I.A.; Vrublevska, J.; Sepp, T.; Abolins-Abols, M.; Rantala, M.J.; Mierauskas, P.; Krama, T. | (161) |

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| P114 | 2017 | Consistent variation in individual migration strategies of brown skuas | Krietsch, J.; Hahn, S.; Kopp, M.; Phillips, R.A.; Peter, H.-U.; Lisovski, S. | (162) |
| P115 | 2017 | The transition to independence: sex differences in social and behavioural development of wild bottlenose dolphins | Krzyszczuk, E.; Patterson, E.M.; Stanton, M.A.; Mann, J. | (163) |
| P116 | 2017 | Comparative analysis of the brain transcriptome in a hyper-aggressive fruit fly, <i>Drosophila prolongata</i> | Kudo, A.; Shigenobu, S.; Kadota, K.; Nozawa, M.; Shibata, T.F.; Ishikawa, Y.; Matsuo, T. | (164) |
| P117 | 2014 | U-shaped relationship between ageing and risk-taking behaviour in a wild-type rodent | Lafaille, M.; Féron, C. | (165) |
| P118 | 2015 | Social Conditioned Place Preference in the Captive Ground Squirrel (<i>Ictidomys tridecemlineatus</i>): Social Reward as a Natural Phenotype | Lahvis, G.P.; Panksepp, J.B.; Kennedy, B.C.; Wilson, C.R.; Merriman, D.K. | (166) |
| P119 | 2014 | Effects of a post-weaning cafeteria diet in young rats: Metabolic syndrome, reduced activity and low anxiety-like behaviour | Lalanza, J.F.; Caimari, A.; Del Bas, J.M.; Torregrosa, D.; Cigarroa, I.; Pallás, M.; Capdevila, L.; Arola, L.; Escorihuela, R.M. | (167) |
| P120 | 2015 | Temporally fluctuating selection on a personality trait in a wild rodent population | Le Cœur, C.; Thibault, M.; Pisanu, B.; Thibault, S.; Chapuis, J.-L.; Baudry, E. | (168) |
| P122 | 2017 | Males are quicker to adjust aggression towards heterospecific intruders in a cichlid fish | Lehtonen, T.K.; Wong, B.B.M. | (169) |
| P123 | 2011 | Better the devil you know: Familiarity affects foraging activity of red-backed salamanders, <i>Plethodon cinereus</i> | Liebgold, E.B.; Dibble, C.J. | (170) |
| P124 | 2018 | Behavioral differences in an over-invasion scenario: marbled vs. spiny-cheek crayfish | Linzmaier, S.M.; Goebel, L.S.; Ruland, F.; Jeschke, J.M. | (171) |
| P125 | 2014 | The influence of mitonuclear genetic variation on personality in seed beetles | Løvlie, H.; Immonen, E.; Gustavsson, E.; Kazancioğlu, E.; Arnqvist, G. | (172) |
| P127 | 2017 | Sex composition modulates the effects of familiarity in new environment | Lucon-Xiccato, T.; Mazzoldi, C.; Griggio, M. | (173) |
| P128 | 2002 | Risk taking during exploration of a plus-maze is greater in adolescent than in juvenile or adult mice | Macri, S.; Adriani, W.; Chiarotti, F.; Laviola, G. | (174) |
| P129 | 2015 | Exploratory and defensive behaviours change with sex and body size in eastern garter snakes (<i>Thamnophis sirtalis</i>) | Maillet, Z.; Halliday, W.D.; Blouin-Demers, G. | (175) |
| P130 | 2011 | Zebra finches are bolder in an asocial, rather than social, context | Mainwaring, M.C.; Beal, J.L.; Hartley, I.R. | (176) |
| P131 | 2013 | Hatching asynchrony and offspring sex influence the subsequent exploratory behaviour of zebra finches | Mainwaring, M.C.; Hartley, I.R. | (177) |
| P132 | 2012 | Altered Prey Responses in Round Goby from Contaminated Sites | Marentette, J.R.; Balshine, S. | (178) |
| P133 | 2015 | Maternal rank influences the outcome of aggressive interactions between immature chimpanzees | Markham, A.C.; Lonsdorf, E.V.; Pusey, A.E.; Murray, C.M. | (179) |
| P134 | 2012 | Exploring novelty: A component trait of behavioural syndromes in a colonial fish | Martins, C.I.M.; Schaedelin, F.C.; Mann, M.; Blum, C.; Mandl, I.; Urban, D.; Grill, J.; Schöbwendler, J.; Wagner, R.H. | (180) |

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| P135 | 2015 | Does metabolic rate predict risk-taking behaviour? A field experiment in a wild passerine bird | Mathot, K.J.; Nicolaus, M.; Araya-Ajoy, Y.G.; Dingemanse, N.J.; Kempenaers, B. | (181) |
| P136 | 2002 | Developmental changes in responsiveness to parents and unfamiliar adults in a monogamous monkey (<i>Callicebus moloch</i>) | Mayeaux, D.J.; Mason, W.A.; Mendoza, S.P. | (182) |
| P137 | 2014 | Nestling activity levels during begging behaviour predicts activity level and body mass in adulthood | McCowan, L.S.C.; Griffith, S.C. | (183) |
| P138 | 2015 | Active but asocial: Exploration and activity is linked to social behaviour in a colonially breeding finch | McCowan, L.S.C.; Griffith, S.C. | (184) |
| P139 | 2018 | Thermal parental effects on offspring behaviour and their fitness consequences | McDonald, S.; Schwanz, L.E. | (185) |
| P140 | 2003 | The evolution of movements and behaviour at boundaries in different landscapes: A common arena experiment with butterflies | Merckx, T.; Van Dyck, H.; Karlsson, B.; Leimar, O. | (186) |
| P141 | 2016 | Are behavioural syndromes sex specific? Personality in a widespread lizard species | Michelangeli, M.; Chapple, D.G.; Wong, B.B.M. | (187) |
| P143 | 2014 | Pulsed resources and the coupling between life-history strategies and exploration patterns in eastern chipmunks (<i>Tamias striatus</i>) | Montiglio, P.-O.; Garant, D.; Bergeron, P.; Messier, G.D.; Reale, D. | (188) |
| P144 | 2010 | Individual variation in temporal activity patterns in open-field tests | Montiglio, P.-O.; Garant, D.; Thomas, D.; Reale, D. | (189) |
| P145 | 2013 | Weevil x Insecticide: Does 'personality' matter? | Morales, J.A.; Cardoso, D.G.; Della Lucia, T.M.C.; Guedes, R.N.C. | (190) |
| P149 | 2007 | Behavioral syndromes and the evolution of correlated behavior in zebrafish | Moretz, J.A.; Martins, E.P.; Robison, B.D. | (191) |
| P150 | 2015 | Sex, boldness and stress experience affect convict cichlid, <i>Amatitlania nigrofasciata</i> , open field behaviour | Moscicki, M.K.; Hurd, P.L. | (192) |
| P151 | 2018 | Inbreeding affects personality and fitness of a leaf beetle | Müller, T.; Juškauskas, A. | (193) |
| P152 | 2016 | Effects of larval versus adult density conditions on reproduction and behavior of a leaf beetle | Müller, T.; Küll, C.L.; Müller, C. | (194) |
| P154 | 2013 | Parental provisioning behaviour plays a key role in linking personality with reproductive success | Mutzel, A.; Dingemanse, N.J.; Araya-Ajoy, Y.G.; Kempenaers, B. | (195) |
| P155 | 2010 | A behavioral syndrome in the adzuki bean beetle: Genetic correlation among death feigning, activity, and mating behavior | Nakayama, S.; Miyatake, T. | (196) |
| P156 | 2010 | Genetic correlation between behavioural traits in relation to death-feigning behaviour | Nakayama, S.; Nishi, Y.; Miyatake, T. | (197) |
| P157 | 2012 | Dopaminergic system as the mechanism underlying personality in a beetle | Nakayama, S.; Sasaki, K.; Matsumura, K.; Lewis, Z.; Miyatake, T. | (198) |
| P159 | 2010 | Biogenic amines, caffeine and tonic immobility in <i>Tribolium castaneum</i> | Nishi, Y.; Sasaki, K.; Miyatake, T. | (199) |
| P160 | 2015 | Context matters: Multiple novelty tests reveal different aspects of shyness-boldness in farmed American mink (<i>Neovison vison</i>) | Noer, C.L.; Needham, E.K.; Wiese, A.-S.; Balsby, T.J.S.; Dabelsteen, T. | (200) |
| P162 | 2018 | Sun-basking fish benefit from body temperatures that are higher than ambient water | Nordahl, O.; Tibblin, P.; Koch-Schmidt, P.; Berggren, H.; Larsson, P.; Forsman, A. | (201) |

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| P165 | 2013 | Differences in boldness are repeatable and heritable in a long-lived marine predator | Patrick, S.C.; Charmantier, A.; Weimerskirch, H. | (202) |
| P166 | 2011 | Factors affecting aggression in a captive flock of Chilean flamingos (<i>Phoenicopterus chilensis</i>) | Perdue, B.M.; Gaalema, D.E.; Martin, A.L.; Dampier, S.M.; Maple, T.L. | (203) |
| P167 | 2014 | Does sex influence intraspecific aggression and dominance in Nile tilapia juveniles? | Pinho-Neto, C.F.; Miyai, C.A.; Sanches, F.H.C.; Giaquinto, P.C.; Delicio, H.C.; Barcellos, L.J.G.; Volpato, G.L.; Barreto, R.E. | (204) |
| P169 | 2014 | Precocial bird mothers shape sex differences in the behavior of their chicks | Pittet, F.; Houdelier, C.; Lumineau, S. | (205) |
| P170 | 2010 | Sex matters: A social context to boldness in guppies (<i>Poecilia reticulata</i>) | Piyapong, C.; Krause, J.; Chapman, B.B.; Ramnarine, I.W.; Louca, V.; Croft, D.P. | (206) |
| P171 | 2008 | Novel environmental enrichment may provide a tool for rapid assessment of animal personality: A case study with giant pandas (<i>Ailuropoda melanoleuca</i>) | Powell, D.M.; Svoke, J.T. | (207) |
| P173 | 2014 | Sociality and oxytocin and vasopressin in the brain of male and female dominant and subordinate mandarin voles | Qiao, X.; Yan, Y.; Wu, R.; Tai, F.; Hao, P.; Cao, Y.; Wang, J. | (208) |
| P175 | 2008 | Juvenile female aggression in cooperatively breeding pied babblers: causes and contexts | Raihani, N.J.; Ridley, A.R.; Browning, L.E.; Nelson-Flower, M.J.; Knowles, S. | (209) |
| P177 | 2017 | Predation environment affects boldness temperament of neotropical livebearers | Rasmussen, J.E.; Belk, M.C. | (210) |
| P178 | 2008 | Aggression, sex and individual differences in cerebral lateralization in a cichlid fish | Reddon, A.R.; Hurd, P.L. | (211) |
| P179 | 2016 | A time to wean? Impact of weaning age on anxiety-like behaviour and stability of behavioural traits in full adulthood | Richter, S.H.; K_ stner, N.; Lodenkemper, D.-H.; Kaiser, S.; Sachser, N. | (212) |
| P180 | 2018 | The function of ultrasonic vocalizations during territorial defence by pair-bonded male and female California mice | Rieger, N.S.; Marler, C.A. | (213) |
| P181 | 2014 | Sex-specific differences in offspring personalities across the laying order in magpies <i>Pica pica</i> | Rokka, K.; Pihlaja, M.; Siitari, H.; Soulsbury, C.D. | (214) |
| P182 | 2018 | Phenotypic determinants of inter-individual variability of litter consumption rate in a detritivore population | Rota, T.; Jabiol, J.; Chauvet, E.; Lecerf, A. | (215) |
| P183 | 2018 | Population, sex and body size: Determinants of behavioural variations and behavioural correlations among wild zebrafish <i>Danio rerio</i> | Roy, T.; Bhat, A. | (216) |
| P184 | 2015 | Under the influence: Sublethal exposure to an insecticide affects personality expression in a jumping spider | Royaute, R.; Buddle, C.M.; Vincent, C. | (217) |
| P186 | 2012 | The development of exploratory behaviour in the African striped mouse <i>Rhabdomys</i> reflects a gene x environment compromise | Rymer, T.L.; Pillay, N. | (218) |
| P187 | 2017 | Impacts of the antidepressant fluoxetine on the anti-predator behaviours of wild guppies (<i>Poecilia reticulata</i>) | Saaristo, M.; McLennan, A.; Johnstone, C.P.; Clarke, B.O.; Wong, B.B.M. | (219) |
| P188 | 2017 | How to be a great dad: parental care in a flock of greater flamingo (<i>Phoenicopterus roseus</i>) | Sandri, C.; Vallarin, V.; Sammarini, C.; Regaiolli, B.; Piccirillo, A.; Spiezio, C. | (220) |

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| P189 | 2018 | Habitat-dependent effects of personality on survival and reproduction in red squirrels | Santicchia, F.; Gagnaison, C.; Bisi, F.; Martinoli, A.; Matthysen, E.; Bertolino, S.; Wauters, L.A. | (221) |
| P190 | 2010 | Novelty-Seeking Temperament in Captive Stumptail Macaques (<i>Macaca arctoides</i>) and Spider Monkeys (<i>Ateles geoffroyi</i>) | Santillán-Doherty, A.M.; Cortés-Sotres, J.; Arenas-Rosas, R.V.; Márquez-Arias, A.; Cruz, C.; Medellín, A.; Aguirre, A.J.; Muñoz-Delgado, J.; Díaz, J.L. | (222) |
| P191 | 2018 | Predictability is attractive: Female preference for behaviourally consistent males but no preference for the level of male aggression in a bi-parental cichlid | Scherer, U.; Kuhnhardt, M.; Schuett, W. | (223) |
| P192 | 2018 | Ground beetles in city forests: Does urbanization predict a personality trait? | Schuett, W.; Delfs, B.; Haller, R.; Kruber, S.; Roölfs, S.; Timm, D.; Willmann, M.; Drees, C. | (224) |
| P193 | 2010 | Life history and behavioral type in the highly social cichlid <i>Neolamprologus pulcher</i> | Schürch, R.; Heg, D. | (225) |
| P194 | 2017 | Repeatability and consistency of individual behaviour in juvenile and adult Eurasian harvest mice | Schuster, A.C.; Carl, T.; Foerster, K. | (226) |
| P195 | 2005 | Aggression in bottlenose dolphins: Evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour | Scott, E.M.; Mann, J.; Watson-Capps, J.J.; Sargeant, B.L.; Connor, R.C. | (227) |
| P196 | 2017 | Are there consistent behavioral differences between sexes and male color morphs in <i>Pelvicachromis pulcher</i> ? | Seaver, C.M.S.; Hurd, P.L. | (228) |
| P197 | 2006 | Habitat exploration and use in dispersing juvenile flying squirrels | Selonen, V.; Hanski, I.K. | (229) |
| P200 | 2009 | Intersexual differences in European lobster (<i>Homarus gammarus</i>): Recognition mechanisms and agonistic behaviours | Skog, M. | (230) |
| P201 | 2009 | Sex differences in the social behavior of wild spider monkeys (<i>Ateles geoffroyi yucatanensis</i>) | Slater, K.Y.; Schaffner, C.M.; Aureli, F. | (231) |
| P202 | 2006 | Social partner preferences of male and female fighting fish (<i>Betta splendens</i>) | Snekser, J.L.; McRobert, S.P.; Clotfelter, E.D. | (232) |
| P203 | 2018 | Risk-taking behavior, urbanization and the pace of life in birds | Sol, D.; Maspons, J.; Gonzalez-Voyer, A.; Morales-Castilla, I.; Garamszegi, L.Z.; Möller, A.P. | (233) |
| P204 | 2010 | Preferences for limited versus no contact in SD rats | Sørensen, D.; Hanse, H.; Krohn, T.; Bertelsen, T. | (234) |
| P205 | 2012 | Individual and sex-based differences in behaviour and ecology of rat snakes in winter | Sperry, J.H.; Weatherhead, P.J. | (235) |
| P206 | 2017 | Personality in the cockroach <i>Diploptera punctata</i> : Evidence for stability across developmental stages despite age effects on boldness | Stanley, C.R.; Mettke-Hofmann, C.; Preziosi, R.F. | (236) |
| P207 | 2009 | Dichotomies in perceived predation risk of drinking wallabies in response to predatory crocodiles | Steer D.; Doody, J.S. | (237) |
| P211 | 2015 | Sex differences in exploratory behaviour of laboratory CD-1 mice (<i>Mus musculus</i>) | Tanaka, T. | (238) |

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| P212 | 2014 | Behavioral Responses to Social Separation Stressor Change Across Development and Are Dynamically Related to HPA Activity in Marmosets | Taylor, J.H.; Mustoe, A.C.; French, J.A. | (239) |
| P213 | 1988 | Sex differences in investigatory and grooming behaviors of laboratory rats (<i>Rattus norvegicus</i>) following exposure to novelty | Thor, D.H.; Harrison, R.J.; Schneider, S.R.; Carr, W.J. | (240) |
| P214 | 2018 | Individual behavioral variation reflects personality divergence in the upcoming model organism <i>Nothobranchius furzeri</i> | Thoré, E.S.J.; Steenaerts, L.; Philippe, C.; Grégoir, A.; Brendonck, L.; Pinceel, T. | (241) |
| P215 | 2013 | Dear enemies and nasty neighbors in crayfish: Effects of social status and sex on responses to familiar and unfamiliar conspecifics | Tierney, A.J.; Andrews, K.; Happer, K.R.; White, M.K.M. | (242) |
| P216 | 2014 | Effect of predation threat on repeatability of individual crab behavior revealed by mark-recapture | Toscano, B.J.; Gatto, J.; Griffen, B.D. | (243) |
| P217 | 2018 | Does it always pay to defend one's nest? A case study in African penguin | Traisnel, G.; Pichegru, L. | (244) |
| P218 | 2013 | Individual differences in activity levels in zebrafish (<i>Danio rerio</i>) | Tran, S.; Gerlai, R. | (245) |
| P219 | 2012 | Is the exploratory behavior of <i>Liolaemus nitidus</i> modulated by sex? | Troncoso-Palacios, J.; Labra, A. | (246) |
| P220 | 2003 | Are the effects of different enrichment designs on the physiology and behaviour of DBA/2 mice consistent? | Tsai, P.P.; Stelzer, H.D.; Hedrich, H.J.; Hackbarth, H. | (247) |
| P221 | 2018 | House sparrows' (<i>Passer domesticus</i>) behaviour in a novel environment is modulated by social context and familiarity in a sex-specific manner | Tuliozi, B.; Fracasso, G.; Hoi, H.; Griggio, M. | (248) |
| P222 | 2015 | Hidden semi-Markov models reveal multiphasic movement of the endangered Florida panther | van de Kerk, M.; Onorato, D.P.; Criffield, M.A.; Bolker, B.M.; Augustine, B.C.; McKinley, S.A.; Oli, M.K. | (249) |
| P223 | 2017 | Differential participation in cognitive tests is driven by personality, sex, body condition and experience | van Horik, J.O.; Langley, E.J.G.; Whiteside, M.A.; Madden, J.R. | (250) |
| P224 | 2015 | No evidence for correlational selection on exploratory behaviour and natal dispersal in the great tit | van Overveld, T.; Adriaensen, F.; Matthysen, E. | (251) |
| P225 | 2014 | Seasonal- and sex-specific correlations between dispersal and exploratory behaviour in the great tit | van Overveld, T.; Careau, V.; Adriaensen, F.; Matthysen, E. | (252) |
| P226 | 2017 | Sex-specific phenotypes and metabolism-related gene expression in juvenile sticklebacks | Velando, A.; Costa, M.M.; Kim, S.-Y. | (253) |
| P227 | 2011 | Social control of unreliable signals of strength in male but not female crayfish, <i>Cherax destructor</i> | Walter, G.M.; Van Uitregt, V.O.; Wilson, R.S. | (254) |
| P229 | 2015 | Genetic sources of individual variation in parental care behavior | Wetzel, D.P.; Hatch, M.I.; Westneat, D.F. | (255) |
| P230 | 2014 | Parental care syndromes in house sparrows: Positive covariance between provisioning and defense linked to parent identity | Wetzel, D.P.; Westneat, D.F. | (256) |
| P231 | 2016 | Behavioral repeatability of flour beetles before and after metamorphosis and throughout aging | Wexler, Y.; Subach, A.; Pruitt, J.N.; Scharf, I. | (257) |
| P232 | 2017 | Activity syndromes and metabolism in giant deep-sea isopods | Wilson, A.D.M.; Szekeres, P.; Violich, M.; Gutowsky, L.F.G.; Eliason, E.J.; Cooke, S.J. | (258) |

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| P233 | 2010 | Behavioral correlations across activity, mating, exploration, aggression, and antipredator contexts in the European house cricket, <i>Acheta domesticus</i> | Wilson, A.D.M.; Whattam, E.M.; Bennett, R.; Visanuvimol, L.; Lauzon, C.; Bertram, S.M. | (259) |
| P234 | 2013 | Causes and consequences of contest outcome: Aggressiveness, dominance and growth in the sheephead swordtail, <i>Xiphophorus birchmanni</i> | Wilson, A.J.; Grimmer, A.; Rosenthal, G.G. | (260) |
| P235 | 1996 | Agonistic and sensory behaviour of the salamander <i>Ensatina eschscholtzii</i> during asymmetrical contests | Wiltenmuth, E.B. | (261) |
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| P237 | 2012 | Comparing behavioral responses across multiple assays of stress and anxiety in zebrafish (<i>Danio rerio</i>) | Wong, R.Y.; Perrin, F.; Oxendine, S.E.; Kezios, Z.D.; Sawyer, S.; Zhou, L.; Dereje, S.; Godwin, J. | (263) |
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