# **Sex differences and variability in animal personalities: a meta-analysis**

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## *Background ­*

In human psychology there are five categories in which our behavioural quirks, or personalities, can be grouped: Extraversion, Neuroticism, Conscientiousness, Agreeableness and Openness (Nettle 2007). These ‘big five’ factors consistently group correlated behaviours together to give a surprisingly accurate picture of how we see and react to the world. Such consistent, personality-like behaviours are not just a human quirk - animal behaviour often varies between individuals of the same species even under the same set of conditions (Dall *et al.* 2004, Roche *et al.* 2016). For example, individuals within a population might differ in their aggressiveness towards each other; although these individuals might alter their aggression according to the situation (i.e. their opponent, hunger levels), some will still be consistently more aggressive than others. And, like human personalities, suites of correlated, consistent behaviours (called behavioural syndromes; Sih *et al*. 2004) can be grouped into categories that resemble the human ‘big five’: Activity, Exploration, Boldness, Aggression and Sociality (Réale *et al.* 2007).

For organisms living in the wild, consistent and predictable (i.e. repeatable) behaviour across time and contexts seems maladaptive, especially when there is such large inter-individual variation in response to the same environmental conditions (Dingemanse *et al.* 2010). However, the consistency of personality within individuals, and its persistence across generations, suggests that low intra-individual variation can be adaptive (Smith & Blumstein 2008; Dingemanse & Wolf 2010). For example, little variation in a male’s aggressive behaviour can be an honest signal of his competitive ability, so consistency can be favoured when females want to make good decisions about potential mates. Such individual consistency in personality can be maintained by sexual selection via non-random mate choice (e.g. female guppies prefer bold males; Godin & Dugatkin 1996), or male-male competition (Schuett *et al*. 2010). For example, in a meta-analytic study of humans, Budaev (1999) found that the Agreeableness/Neuroticism behavioural syndrome explains dominance-related aggression in men and is likely maintained by frequency-dependent selection.

Under sexual selection, the sex with the greatest variation in their mating success (often males) should also have greater variation in traits used to obtain matings (e.g. weapons, signalling behaviour) (Darwin 1871; but see Mackenzie *et al.* 1995). Furthermore, theory suggests that the heterogametic sex (the sex with one copy of each sex chromosome) might be the most variable, particularly when considering traits under sexual selection (the ‘sex-chromosome hypothesis’; see Reinhold & Engqvist 2013 for review). For example, mammalian females carry two copies of the X-chromosome, so traits influenced by X-chromosome genes will be averaged across two parental copies, whereas males have only one X-chromosome so the effect of the same genes will not be averaged (Reinhold & Engqvist 2013). To date the sex-chromosome hypothesis has mostly been related to explaining sexual size dimorphism, yet the idea that one sex is more variable than the other can also be extended to include behaviours because they too have a genetic underpinning (Dochtermann *et al.* 2014). For example, paternal care and territorial aggression are male behaviours that influence female mate choice, so greater variation in the expression of those behaviours among males than females is predicted (see Schuett *et al*. 2010 for review). When males and females share behavioural syndromes, sex-specific differences in their expression can lead to different fitness consequences. For example, male and female comb-footed spiders (*Anelosimus studiosus*) share the same aggressive-social behavioural syndrome, but aggressive males have better mating success than social males, while social females have better mating success than aggressive females (Pruitt & Riechert 2009).

Although the knowledge gap regarding sex differences in personality and consistency has been acknowledged (Schuett *et al.* 2010; Garamszegi *et al.* 2012; Tarka *et al.* 2018), only a handful of studies since consider males and females separately when studying personality (e.g. Chapman *et al.* 2013; Strickland *et al.* 2014; Michelangeli *et al.* 2016; Scherer *et al*. 2018). To address the knowledge gap, we conducted a systematic review and meta-analysis to investigate: 1) do the sexes differ in their mean expression of personality, and 2) is there a sex-specific pattern of across-individual variation across phyla? That is, are males always the more variable sex when we examine personality-like behaviours?

## *Experimental Methodology*

We conducted a systematic review and meta-analysis by systematically searching the literature for empirical studies that include the mean and variation for different animal personality traits (as classified by Sih *et al*. 2004 & Réale *et al*. 2007) of both males and females. We chose to only include studies that provided means and error because model estimates may not reflect the true variation. Likewise, studies that only report PCAs and factor loadings will also be excluded for the same reason (see Figure 2).

We collected 10,9991 papers from both Web of Science and Scopus databases in December 2018, using a primary and secondary keyword search (see Figure 3), as well as including every paper that has cited one of five key personality reviews: (Dall *et al.* 2004; Sih *et al.* 2004; Réale *et al.* 2007; Schuett *et al.* 2010; Dingemanse & Wolf 2010). A secondary search was used to find and include studies that studied personality-like behaviours that were not defined as personalities. Of the 10,991 total studies, only 3,737 were not duplicates. This is still a far more comprehensive literature search than the most recent personality meta-analysis, which had 1,431 studies in total (including results from another, unrelated search topic: see Tarka *et al.* 2018). I have scanned 2,950 full text articles to get 245 eligible studies (see Figure 3). I am currently collecting raw means, error and sample sizes for each sex/personality trait from those eligible studies for Aims 1 & 3.



**Figure 2.** *Preferred Reporting Items for Systematic Reviews and Meta-Analyses* (*PRISMA*) pipeline showing my inclusion/exclusion criteria when scanning abstracts in *Rayyan* (Ouzzani *et al.* 2016).

Our meta-analytic models will split the data into the five personality types separately in order to see how males and females differ – the five types suggested by Réale *et al.* (2007); Boldness, Aggression, Activity, Sociality and Exploration. This meta-analysis will also include the following moderator terms:

* Taxonomic group – invertebrates, fish, amphibians, reptiles, birds, marsupials and mammals to look for patterns across taxa. If necessary some of these groupings will be combined to ensure sensible sample sizes
* Phylogenetic relatedness information (branch lengths from reconstructed trees) - to account for phylogenetic non-independence and taxonomic bias
* Age (juveniles or adults) – if there are sex differences, are they more apparent after sexual maturity?
* Field vs lab measurements – to compare measurements made in experimental (manipulated) and observational studies
* Body size (sexual size dimorphism index), mating system, and parental care (to see how sex differences in the mean and variation in personality traits correspond with the likely level of sexual selection (i.e. to compare results with those reported by Reinhold & Engqvist (2013) regarding sexual size dimorphism)
* Study ID – random effect to control for variation within and between studies

Where body size measures for males and females, mating system and parental care were not reported in the primary literature, we then conducted another literature search using Web of Science, Scopus and Google Scholar. We used the search terms: “species name” AND male AND female AND body size OR length (for body size measures), “species name” AND parental care OR mating system for parental care and mating system. Finally, if the final dataset contains moderators with fewer than 2 effect sizes per level (or a number that is inappropriate for analysis), they might be removed from further analysis.

## *Statistical Methodology*

*Mean and variance*

Because this meta-analysis will be comparing the mean and the variance around the mean (error), and their relationship, we plan to analyse sex differences (where *C* are males, *E* are females) in personality means using the natural logarithm of response ratio (lnRR) method. The lnRR method transforms data on a logarithmic scale so it is more normally distributed around zero, thus zero becomes the null hypothesis (no difference between males and females) to test for differences in mean personality between males and females (see Nakagawa *et al.* 2015):

Further, we will analyse the mean-variance relationship using the natural logarithm coefficient of variation ratio (lnCVR):

where CV*E* and CV*C* are *SE /E*  and *SC /C*  , respectively (from Nakagawa *et al.* 2015).

However, if the mean-variance relationship does not fit expected patterns (i.e. when the error is not proportional to the mean across studies – follows Taylor’s law), then the mean and error will be log-transformed to σ (see Nakagawa *et al.* 2015):

Where is the *j*th effect size, is the mean estimate for the *j*th effect size, *Group* is a binary variable for comparing groups (i.e. control = 0, treatment = 1), is the intercept, is the slope or regression coefficient for *Group* (i.e. the difference between control and treatment groups), is the slope or regression coefficient for the mean estimate, is the random intercept (deviation from ), (random slope) is the deviation from , and have a multivariate normal distribution with the variance-covariance, and is the *j*th residual value which is normally distributed with , is sampling error effect for the *j*th effect size (again, see Nakagawa *et al*. 2015 for more details).

This statistical method for calculating mean-variance across studies has been used previously in a meta-analytic framework (see O’Dea *et al.* 2018). Meta-analytic models will be created using the R package *metafor* (Viechtbauer 2010) – *metafor* calculates and reports heterogeneity (*I*2) which will be used as a measure of consistency in this meta-analysis (Noble *et al.* 2017).

Where appropriate, means and error reported as proportions will be transformed using methods reported by Tarka *et al*. (2018). This is because upper-and lower bound proportions (close to 1 or to 0) will have constrained error compared to mid-range proportions and so won’t truly reflect the variation of individuals that possess personality traits at the higher or lower ends of the continuum. Standard deviation (SD) will be our chosen measure of variation, so studies that report standard error as error will be converted to SD.

*Phylogeny & Non-Independence*

Additionally, it is likely that the studies included in our analysis may show statistical non-independence because multiple studies often use the same handful of model species (same cohort, Nakagawa *et al*. 2017), and because sampling is taxonomically-biased (i.e. many bird but fewer insect studies). If this is the case then establishing phylogenetic relatedness can also be useful for controlling for potential bias (e.g. Tarka *et al*. 2018). Phylogenetic trees will be constructed using the R package *rotl* (Michonneau *et al.* 2016) – *rotl* uses updated trees from the Open Tree of Life (opentreeoflife.org/; Hinchliff *et al.* 2015) to obtain the branch lengths for each species (assuming the Brownian Motion model of evolution) which can then be incorporated into meta-analytic models as a moderator term. In this meta-analysis we plan to analyse taxonomic groups separately within the same model.

Where the same study reports mean and error for the same personality trait more than once, report personality measures of the same individuals over different time periods, or in different environments (multiple measures), we plan to collect these multiple effect sizes and will use studyID as a random factor to account for within-study non-independence.

*Publication bias*

We will collect data on author names, year published, and journal name to look for publication bias across studies within the final dataset. Publication bias will be assessed using a sensitivity analysis that also reports heterogeneity (*I*2), which will show the amount of variation not explained by sampling error among studies (Noble *et al.* 2017). However, we will also use the following tests to assess publication bias: funnel plots, QQ plots, Egger regression test and time-lag bias test to see if effect sizes change over time. If some studies are of poorer quality than the rest, we can either weight those studies as less important than better quality studies in the meta-analysis or remove them from further analysis.

*Pre-Registration – PRISMA Protocol*

This meta-analysis has been pre-registered following the preferred reporting items for systematic reviews and meta-analyses protocol (PRISMA; Moher *et al.* 2009) for transparency and has also been checked against suggested reporting guidelines specifically for meta-analyses in the fields of ecology and evolution (O’Dea *et al*. unpublished). The pre-registered protocol is available to view at the Open Science Framework: <https://osf.io/b9ju6/> - Pre-registration of meta-analytic aims and methods allows studies to be transparent to help prevent publication bias and *p* hacking.



3,734

784

245

245

2,705

2,950

10,991

7,257

182

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

*References*

Budaev, S. V. (1999). Sex differences in the Big Five personality factors: Testing an evolutionary hypothesis. *Pers. Individ. Dif.*, 26, 801–813.

Chapman, B.B., Hegg, A. & Ljungberg, P. (2013). Sex and the Syndrome: Individual and Population Consistency in Behaviour in Rock Pool Prawn Palaemon elegans. *PLoS One*, 8, 1–7.

Dall, S.R.X., Houston, A.I. & McNamara, J.M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecol. Lett.*, 7, 734–739.

Darwin, C. (1871). *The descent of man, and selection in relation to sex*. Murray, London.

Dingemanse, N.J., Kazem, A.J.N., Réale, D. & Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol. Evol.*, 25, 81–89.

Dingemanse, N.J. & Wolf, M. (2010). Recent models for adaptive personality differences: A review. *Philos. Trans. R. Soc. B Biol. Sci.*, 365, 3947–3958.

Dochtermann, N.A., Schwab, T. & Sih, A. (2014). The contribution of additive genetic variation to personality variation: Heritability of personality. *Proc. R. Soc. B Biol. Sci.*, 282.

Garamszegi, L.Z., Markó, G. & Herczeg, G. (2012). A meta-analysis of correlated behaviours with implications for behavioural syndromes: Mean effect size, publication bias, phylogenetic effects and the role of mediator variables. *Evol. Ecol.*, 26, 1213–1235.

Godin, J.-G.J. & Dugatkin, L.A. (1996). Female mating preference for bold males in the guppy, Poecilia reticulata. *P.N.A.S.*, 93, 10262–10267.

Hinchliff, C.E., Smith, S.A., Allman, J.F., Burleigh, J.G., Chaudhary, R., Coghill, L.M., *et al.* (2015). Synthesis of phylogeny and taxonomy into a comprehensive tree of life. *Proc. Natl. Acad. Sci.*, 112, 12764–12769.

Mackenzie, A., Reynolds, J.D., Brown, V.J. & Sutherland, W.J. (1995). Variation in Male Mating Success on Leks. *Am. Nat.*, 145, 633–652.

Michelangeli, M., Chapple, D.G. & Wong, B.B.M. (2016). Are behavioural syndromes sex specific? Personality in a widespread lizard species. *Behav. Ecol. Sociobiol.*, 70, 1911–1919.

Michonneau, F., Brown, J.W. & Winter, D.J. (2016). rotl: an R package to interact with the Open Tree of Life data. *Methods Ecol. Evol.*, 7, 1476–1481.

Moher, D., Liberati, A., Tetzlaff, J., Altman, D.G. & The PRISMA Group. (2009). Preferred Reporting Items for Systematic Reviews and Meta-Analyses: The PRISMA Statement. *Ann. Intern. Med.*, 151, 264–269.

Nakagawa, S., Poulin, R., Mengersen, K., Reinhold, K., Engqvist, L., Lagisz, M., *et al.* (2015). Meta-analysis of variation: Ecological and evolutionary applications and beyond. *Methods Ecol. Evol.*, 6, 143–152.

Nettle, D. (2007). *Personality: what makes you the way you are*. Oxford University Press, New York.

Noble, D.W.A., Lagisz, M., O’dea, R.E. & Nakagawa, S. (2017). Nonindependence and sensitivity analyses in ecological and evolutionary meta-analyses. *Mol. Ecol.*, 2410–2425.

O’Dea, R.E., Lagisz, M., Jennions, M.D. & Nakagawa, S. (2018). Gender differences in individual variation in academic grades fail to fit expected patterns for STEM. *Nat. Commun.*, 9.

Ouzzani, M., Hammady, H., Fedorowicz, Z. & Elmagarmid, A. (2016). Rayyan - a web and mobile app for systematic reviews. *Syst. Rev.*, 5, 210.

Pruitt, J.N. & Riechert, S.E. (2009). Sex matters: sexually dimorphic fitness consequences of a behavioural syndrome. *Anim. Behav.*, 78, 175–181.

Réale, D., Reader, S.M., Sol, D., McDougall, P.T. & Dingemanse, N.J. (2007). Integrating animal temperament within ecology and evolution. *Biol. Rev.*, 82, 291–318.

Reinhold, K. & Engqvist, L. (2013). The variability is in the sex chromosomes. *Evolution (N. Y).*, 67, 3662–3668.

Roche, D.G., Careau, V. & Binning, S.A. (2016). Demystifying animal ‘personality’ (or not): why individual variation matters to experimental biologists. *J. Exp. Biol.*, 219, 3832–3843.

Scherer, U., Kuhnhardt, M. & Schuett, W. (2018). Predictability is attractive: Female preference for behaviourally consistent males but no preference for the level of male aggression in a bi-parental cichlid. *PLoS One*, 13.

Schuett, W., Tregenza, T. & Dall, S.R.X. (2010). Sexual selection and animal personality. *Biol. Rev.*, 85, 217–246.

Sih, A., Bell, A.M. & Johnson, J.C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *TREE*, 19, 372–378.

Smith, B.R. & Blumstein, D.T. (2008). Fitness consequences of personality: A meta-analysis. *Behav. Ecol.*, 19, 448–455.

Strickland, K., Gardiner, R., Schultz, A.J. & Frère, C.H. (2014). The social life of eastern water dragons: Sex differences, spatial overlap and genetic relatedness. *Anim. Behav.*, 97, 53–61.

Tarka, M., Guenther, A., Niemelä, P.T., Nakagawa, S. & Noble, D.W.A. (2018). Sex differences in life history, behavior, and physiology along a slow-fast continuum: a meta-analysis. *Behav. Ecol. Sociobiol.*, 72, 132.

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.*, 36, 1–48.