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

**No evidence males are more variable than females: a meta-analysis of animal personalities**

**Introduction**

*Paragraph 1 – sexual selection and sex differences in variability*

*Intro paragraph should probably talk more about human personalities and their explanations – at least give more background about greater male variability…*

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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