

A meta-analysis of factors influencing the strength of mate choice copying in animals

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Lay summary

Meta-analysis shows that both male and female animals are more likely to copy, rather than avoid, the mate choices of their rivals. We analysed the results of 58 studies testing how animal mate choice is influenced by seeing the choice of a rival. We found that animals do copy the choices of rivals, though copying was strongest in mammals and weakest in invertebrates. Both males and females copied to a similar degree.

Abstract

Mate-choice copying is a form of social learning in which an individual's choice of mate is influenced by the apparent choices of other individuals of the same sex, and has been observed in more than 20 species across a broad taxonomic range. Though fitness benefits of copying have proven difficult to measure, theory suggests that copying should not be beneficial for all species or contexts. However, the factors influencing the evolution and expression of copying have proven difficult to resolve. We systematically searched the literature for studies of mate-choice copying in non-human animals, and then performed a phylogenetically-controlled meta-analysis to explore which factors influence the expression of copying across species. Across 58 published studies in 23 species, we find strong evidence that animals copy the mate choice of others. The strength of copying was significantly influenced by taxonomic group, however sample size limitations mean it is difficult to draw firm conclusions regarding copying in mammals and arthropods. The strength of copying was also influenced by experimental design: copying was stronger when choosers were tested before and after witnessing a conspecific's mate choice, compared to when choosers with social information were compared to choosers without. Importantly, we did not detect any difference in the strength of copying between males and females, or in relation to the rate of multiple mating. Our search also highlights that more empirical work is needed to investigate copying in a broader range of species, especially those with differing mating systems and levels of reproductive investment.

Keywords

Mate choice, mate choice copying, non-independent mate choice, learning, meta-analysis

Introduction

In the natural environment, individuals vary in their quality as a mate, in terms of the resources they can provide to mates, and the parental care or genes they can provide to offspring (Kokko *et al.*, 2003). Because of this, there are often large fitness benefits to choosing the highest-quality mates available via the process of mate choice (Rosenthal, 2017). In social species, interactions between males and females may often be visible to other members of the population. This means that mating, or any other affiliative behaviour, has the potential to create public information which others can use. This information is transmitted inadvertently, making it typically an honest and reliable signal of mate quality (Vakirtzis, 2011). In species with the cognitive ability to recognise and remember such information, there is the potential for observers to use the choices of other individuals of the same sex (referred to as ‘demonstrators’ or ‘models’) to inform their own mating decisions, a process known as mate-choice copying (Pruett-Jones, 1992). Mate-choice copying is a form of social learning in which an individual’s choice of mate is influenced by the apparent choices of other conspecifics of the same sex (Wade & Pruett-Jones, 1990; Dugatkin, 1992). Typically, the attractiveness of a potential partner (which we call the ‘target’ individual) is increased after observing a rival demonstrator interacting positively with the partner. Copying is predicted to reduce the cost associated with sampling mates (Wade & Pruett-Jones, 1990; Vakirtzis, 2011; Dubois *et al.*, 2011), and may be especially advantageous when quality is difficult to assess (Mery *et al.*, 2009; Vakirtzis, 2011) or the copier is inexperienced (Dugatkin and Godin, 1993). Conversely, in some cases copying could lead to poorer choices, if copying causes observers to ignore signals of low quality (Dubois *et al.*, 2011). For example, male guppies (*Poecilia reticulata*) usually prefer larger, more fecund females,

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but in the presence of social information can be led to prefer the smaller of two females (Auld and Godin, 2015).

Theoretically, any species which exhibits mate choice and possesses the cognitive capacity for social learning (Shettleworth, 2010) could exhibit mate-choice copying. To date, mate-choice copying has been recorded in over 20 non-human species, including mammals, birds, fishes, spiders, and insects (Vakirtzis, 2011; Jones & DuVal, 2019). Even species commonly believed to have minimal cognitive abilities, such as the fruit fly *Drosophila melanogaster*, have repeatedly been shown to exhibit mate-choice copying (Mery *et al.*, 2009; Danchin *et al.*, 2018). A subset of studies also find evidence for ‘generalised’ copying, whereby observers apply a newly-observed preference to all mates with the same phenotype as the chosen target individual (Vakirtzis, 2011). This has been seen in fish (Godin *et al.*, 2005; Witte & Noltemeier, 2002), birds (White & Galef, 2000a; Swaddle *et al.*, 2005), and arthropods (Mery *et al.*, 2009; Fowler-Finn *et al.*, 2015). However, a growing number of studies have tested for mate-choice copying and found a non-significant effect (e.g. Lafleur *et al.*, 1997; Auld *et al.*, 2009; Milner *et al.*, 2011). Further, in some species copying has been found in some tests but not others (e.g. guppies *P. reticulata*: Dugatkin, 1992, Lafleur *et al.*, 1997; zebra finches *Taeniopygia guttata*: Doucet *et al.*, 2004, Swaddle *et al.*, 2005). Indeed, a recent meta-analysis has shown quantitatively that the prevalence and strength of copying varies greatly both across and within species (Jones & DuVal, 2019).

This raises the question: what factors influence the evolution or expression of copying? The fitness benefits of copying have proven difficult to measure (Witte *et al.*, 2015), but theory nevertheless predicts that copying will not be advantageous in all contexts and for all species. For example, copying is predicted to increase copier fitness when mate sampling is costly,

quality is difficult to assess, and preferences take time to learn, and should be more likely in species with high sociality and overlapping generations (Varela *et al.*, 2018). Additionally, species which are strictly monogamous, or require biparental care for the successful rearing of offspring, should be less likely to exhibit individual mate-choice copying, because of the high costs associated with sharing mates (Vakirtzis and Roberts, 2009; though note that this cost does not apply to generalised copying). In many cases monogamous species do not copy, as predicted (e.g. Slagsvold and Viljugrein, 1999). However, in other cases, mate-choice copying has been experimentally observed in a number of socially or exclusively monogamous species. These include the monandrous wolf spiders of the genus *Schizocosa* (Norton and Uetz, 2005, Fowler-Finn *et al.*, 2015) and the socially monogamous Japanese quail *Coturnix japonica* (Nichols, 1991). The occurrence of mate-choice copying could also be affected by factors relating to experimental design, either because this influences our ability to measure copying, or because the behaviour of copiers differs between experiments (Dougherty, 2020). For example, studies may also differ in the extent to which the demonstrator is able to interact with the target. Mate-choice copying may occur in response to the observation of mating (e.g. Fowler-Finn *et al.* 2015, Nöbel *et al.*, 2018a) or close affiliation (e.g. Dugatkin and Godin, 1992, Gierzewski *et al.*, 2018) between demonstrators and targets. Given that mating is likely a stronger signal of mate quality than sexual interest or affiliation, observers may be more likely to copy after witnessing an actual mating event compared to the latter behaviours.

The sex of the observer is another factor which is often suggested to influence copying (Witte *et al.*, 2015). Females are assumed to be more likely to copy than males, because the loss of fitness incurred by making an incorrect assessment of mate quality is greater for females, who typically invest more into reproduction than males (Trivers, 1972). Sharing a mate may

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also be more costly for males, because sperm competition reduces male fitness when mating with non-virgin females (Simmons, 2001; Vakirtzis and Roberts, 2009). Nevertheless, evidence for male mate-choice copying has been found in several species (e.g. Schlupp and Ryan, 1997; Wong and McCarthy, 2009; Auld and Godin, 2015; Nöbel *et al.*, 2018a; but see White and Galef, 2000b, Widemo, 2006), though it is unclear whether it is generally weaker than female copying. Notably, male copying in several species may be explained by the fact that males may invest in reproduction as much as, or even more than, females (Widemo, 2006; Moran *et al.*, 2013; Witte *et al.*, 2015; Scauzillo & Ferkin, 2019).

Overall then, there are now a large number of studies that have examined mate-choice copying in animals, and which have shown that the prevalence and strength of copying varies greatly across and even within species. However, the factors driving this variation remain largely unclear. Though traditional reviews can highlight promising areas for study (e.g. Vakirtzis, 2011; Witte *et al.*, 2015; Scauzillo & Ferkin, 2019), a focus on significant or non-significant *P* values can obscure more subtle patterns (Koricheva *et al.*, 2013). By converting the results of these studies into a standardised effect size (rather than *P* values), we can use meta-analysis to test how a range of biological and methodological factors influence the direction (i.e. whether observers copy or avoid the choices of demonstrators) and strength of mate-choice copying. This method was recently used to show that female mate-choice copying in animals is significantly stronger when observers are virgins, when copying is tested in free-living compared to captive subjects, and when demonstrator choice is counter to the observer's preference (Jones & DuVal, 2019).

Here we present the results of a phylogenetically-controlled meta-analysis examining factors influencing the expression of mate-choice copying across animals. We systematically

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surveyed the literature to obtain as many studies as possible examining mate-choice copying in both males and females, across all species excluding humans. This resulted in 158 effect sizes, from 58 studies and 23 species. We then formally test whether a range of biological and methodological factors influence the strength of copying across species. Though our searches resulted in a similar dataset to that used in the recent meta-analysis by Jones & DuVal (2019; and our searches were performed within a month of each other), our study differs in two important ways. First, we explicitly include studies examining mate-choice copying in males, in order to compare the degree of copying between males and females across species. Second, we test the effects of several biological and methodological factors not considered by Jones & DuVal (2019). Taken together, both studies provide a quantitative picture of the current evidence for mate-choice copying across animals, and begin to identify factors which influence the strength of copying.

Methods

Literature search and inclusion criteria

We searched for relevant studies using two main approaches. First, we collected all empirical examples cited in the review of mate-choice copying by Vakirtzis (2011), in addition to all papers citing this review up to the 4th April 2019. Second, we searched the online databases Web of Science and Scopus (on the 4th April 2019) for studies containing the following search terms: “mate choice” AND (copying OR non-independent OR nonindependent OR learning), across all years. We used the ‘Topic’ search field in Web of Science and the ‘Article Title, Abstract, Keywords’ search field in Scopus. This returned 642 results from Web of Science and 552 from Scopus, yielding a total of 1230 papers, reduced to 844 after the removal of duplicates (Figure 1). The titles and abstracts of these papers were then

examined to determine whether they met our inclusion criteria (see below). The numbers of papers rejected, and reasons why, are given in Figure 1. This sorting left 89 papers which were read in their entirety.

A study had to meet several criteria for it to be included in our analysis. First, it must test for mate-choice copying in either females or males. We considered an experiment to test for mate-choice copying if the sexual preference of a focal individual was compared in the presence and absence of social information regarding the preference of a ‘demonstrator’ individual of the same sex. This definition includes studies that do not directly test sexual preferences in the absence of social information, but instead compare post-demonstration preferences to hypothetical values (see below). We excluded studies that were purely observational, did not provide the observer with direct social information (e.g. demonstrator choices inferred from olfactory cues in Kavaliers *et al.*, 2006), or did not compare behaviour to appropriate control data or an appropriate null hypothesis. Strictly-speaking, copying a demonstrator preference could increase or decrease the attractiveness of the target individual (or phenotype), depending on whether the observer witnessed acceptance or rejection by the demonstrator (Pruett-Jones, 1992; Vakirtzis, 2011; Scauzillo & Ferkin, 2019). However, in practice copying of rejection is rarely tested (Scauzillo & Ferkin, 2019), and only one study in our sample tested for an effect of mate rejection on observer behaviour in isolation (Witte & Ueding, 2003). We excluded studies examining forms of learning other than copying, such as social imprinting of sexual preferences (e.g. Bailey & Zuk, 2009). Second, studies needed to provide sufficient data or statistical information to allow us to calculate a standardised effect size. When such information was missing (e.g. missing sample sizes or test statistics), we attempted to contact the authors, requesting either the missing information or the raw data. We obtained the raw data for five studies in this way. Within these limitations, we

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considered studies using a variety of experimental designs (see below). We considered studies in any animal species, excluding humans (for a recent review and meta-analysis of mate-choice copying in humans, see Gouda-Vossos *et al.*, 2018). We considered copying by both males and females. A list of excluded papers, and their reasons for exclusion, is presented in Table S1.

[Fig 1 here]

Effect size calculations

We quantified mate-choice copying as the difference in mating preference in the presence versus absence of social information (social versus control treatment). The greater the difference in preference between treatments, the greater the influence of social information on mate choice. We used the standardised mean difference, known as Hedges' d , as our measure of effect size (Hedges and Olkin, 1985). This effect size is useful because it is easily obtained using a range of different data types (Koricheva *et al.*, 2013). In studies where the focal individual behaved in the same way as the demonstrator, known as 'positive copying', the effect size was given a positive sign. In studies where the focal individual behaved differently to the demonstrator (e.g. when an observer avoids the mate chosen by the demonstrator), known as 'negative copying', the effect size was given a negative sign. All data were extracted by one person (ADD). We extracted all relevant effect sizes from each study. In some cases this resulted in multiple effect sizes for a given study, typically because studies contain multiple experiments or report several behaviours. This potential source of non-independence was controlled for in the analysis (see below).

Effect sizes were calculated from two types of data. First, we used counts of the number of choices made towards each option (2 x 2 contingency table). In these cases we either used chi-squared statistics presented in the text, or performed our own chi square goodness-of-fit tests. The results of chi-squared tests were then converted into d using the equation in Koricheva *et al.* (2013). Second, we used pairs of means representing the average preference in social and control treatments, along with some measure of variance. In this case d can be calculated directly using means, standard deviations, and sample sizes for each treatment group. Means and standard deviations were taken directly from the text, or extracted from figures using Web Plot Digitizer v 4.2 (Rohatgi, 2019). Alternatively, the test statistics from t-tests or paired t-tests were converted into d using the equations in Koricheva *et al.* (2013). Preferences were typically tested using a dichotomous-choice experimental design (Dougherty & Shuker, 2015), resulting in two preference values per test. In these cases we compared the average preference for the option chosen by the demonstrator between the two treatments, or used a difference score if provided by the authors (the difference in association time between the most-preferred and least-preferred options). For preference scores originating from repeated-measures designs (27 effect sizes), the correlation between pre and post-test preferences were generally not reported, and so we assumed a correlation of 0.5 in order to convert paired-t statistics into d . This will underestimate the true effect size slightly if correlations between preferences are typically larger than this (though across species the repeatability of mating preferences is generally low: Bell *et al.*, 2009). For non-parametric data, we converted the z score from a Wilcoxon test (either paired or non-paired) to d using the equation in Koricheva *et al.* (2013). For both types of data, social treatment groups were compared either to control groups, or with a null prediction of random mating (an equal frequency of mating with each choice option, or a difference score of zero) unless other theoretical 'expected' values were specified.

We set the direction of the effect size (positive or negative) following the rules stated above. We also obtained 13 effect sizes with no direction, for two reasons. First, count data can result in a ‘true’ effect size of zero if the frequency of each option does not differ between tests. Second, some studies reported the result of a non-significant statistical test, but provided insufficient information for us to estimate the direction of the effect (e.g. no means provided). These results are typically excluded from meta-analyses (Harts *et al.*, 2016), however this biases the data against non-significant results, which are equally as informative as significant ones. We therefore assigned these effect sizes a value of zero and included them in all analyses, assuming that there is an approximately equal chance that any given result is positive or negative. This is likely conservative, given the fact that positive effect sizes are more common in this dataset (see below). We did this for seven cases.

After the completion of our data collection and statistical analysis the meta-analysis by Jones & DuVal (2019) was published. Coincidentally, the literature searches for the two studies were performed at almost the same time (April and May 2019). This provides the opportunity to assess how, given the same pool of available studies, different research teams may pursue different inclusion criteria and analytical approaches. This is important because meta-analyses may present researchers with an especially large number of subjective choices (“researcher degrees of freedom”: Wicherts *et al.*, 2016; Lakens *et al.*, 2016), which may contribute to cases where two groups have analysed the same literature and got different or conflicting results (e.g. Gildersleeve *et al.*, 2014; Wood *et al.*, 2014; Silberzahn *et al.*, 2015). For illustration, we therefore compare our methodology to that of by Jones & DuVal (2019) in the supplementary material (Table S2).

Moderators and accompanying hypotheses

One aim of this study was to determine which biological and methodological factors influence the direction or strength of copying. For each effect size, we obtained information on the following nine moderator variables:

Biological moderators:

Taxonomic group. The degree of mate-choice copying may differ across taxonomic groups, due to assumed differences in cognitive capacity or sociality. Mate-choice copying has been most commonly investigated in fish and birds, with some tests in mammals and arthropods (including crustaceans, arachnids, and insects). If cognitive capacity is important, we predict that mammals and birds will show the strongest degree of copying, followed by fishes and then arthropods.

Sex. Though copying has been recorded for both males and females, across species we expect copying to be stronger in females, for two reasons. First, females typically invest more in reproduction, and have lower mating rates than males, and so they are under greater selective pressure to make accurate judgements of quality (Mery *et al.*, 2009, Vakirtzis, 2011). Second, males may suffer reduced fertilisation success when mating with recently-mated females due to sperm competition (Simmons, 2001), so that in many species males should actively avoid mating with such females.

Rate of multiple mating. The rate of multiple mating has the potential to influence the costs and benefits of copying, due to effects on the number of future mating opportunities and the degree of competition between rivals. If mating rates are high, copying should be lower because each mating event is less important, and so individuals can be less choosy overall.

Further, both males and females may suffer costs when mating with already-mated members of the opposite sex: from a female perspective, multiply-mated males may be sperm limited (Wedell *et al.*, 2002) or provide less parental resources if they have another brood to care for (Vakirtzis and Roberts, 2009); from a male perspective, multiply-mated females are a high sperm competition risk (Simmons, 2001). We searched the literature for relevant data in order to categorise each species as having either a high or low rate of multiple mating (Table S3). In the first instance we used observations of the number of matings per individual or genetic paternity data to classify species. We classed a species as having a high rate of multiple mating if the majority of broods (>50%) were of mixed paternity, or individuals were observed to mate with an average of two or more partners during a breeding season. For three species we were unable to obtain quantitative estimates of mating rate, but we did find descriptions of the mating system which allowed us to assign species to one of the categories (Table S3). Two species could not be categorised in this way due to a lack of information (the humpbacked limia *Limia nigrofasciata* and the Atlantic molly *Poecilia mexicana*), and mating rate is not relevant to the parthenogenetic Amazon molly *Poecilia formosa* (Schartl *et al.*, 1995), so all three were excluded from the analysis when testing for the effect of this moderator (this applies to nine effect sizes in total).

Animal birth location. The recent meta-analysis by Jones & DuVal (2019) found that copying was significantly stronger in field studies compared to those performed on captive individuals in the lab. This could be because mate sampling is more difficult in the wild, for example because there are more options to choose from, or because the risk of mortality is higher (Jones & DuVal, 2019). However, field studies also have less control over the experience of observers before testing, which could influence both overall mating preferences and the motivation to copy. In order to try to disentangle the effects of previous versus current testing

conditions on copying, we recorded whether individuals used during experiments were born in captivity or in the wild. The birth location has the potential to influence several factors that could influence the strength of copying, such as observer state or social experience (Cotton *et al.*, 2006), and the costs of being choosy (Jennions & Petrie, 1997). We predict that copying will be weaker in wild-caught compared to lab-reared observers, as in the latter category more of these potentially-confounding environmental factors are controlled.

Experimental design moderators:

Individual vs generalised copying. Studies of mate-choice copying typically test how the attractiveness of a specific target individual changes following an observed sexual interaction with a demonstrator (individual copying). Alternatively, copying can lead to the formation of a generalised preference for a specific trait (generalised copying); this is confirmed by testing observer preferences for a different individual, with the same phenotype as the target.

Distinguishing between these two types of copying is important, because they may lead to different ecological or evolutionary outcomes. For example, because a generalised rule can be applied to multiple individuals in a population, generalised copying has a greater potential to lead to widespread cultural transmission of preferences (Vakirtzis, 2011; Danchin *et al.*, 2018). Generalised copying could also potentially aid the spread of novel ornaments in a population (e.g. Mery *et al.*, 2009; Drullion and Dubois, 2008). However, it is not clear whether one type of copying is likely to be stronger than the other. Nevertheless, the two types of copying may require different learning abilities: individual copying requires the ability to recognise and remember specific individuals, whereas generalised copying requires the ability to apply a generalised rule to future mate encounters. It is also noteworthy that few studies have tested for generalised copying in males (Witte *et al.*, 2015; Kniel *et al.*, 2015), and only one of these studies found a significant result (Nöbel *et al.*, 2018a).

Design type. We classified designs as using either a ‘before-and-after’ or a ‘no pre-test’ design. Before-and-after designs test observer preferences twice: once before demonstration and once after demonstration. No pre-test designs test for observer preferences once, following demonstration, and then compare this either to predicted values (e.g. random choice of 50%) or to individuals from a control group that did not witness a demonstration. A difference in copying between these two designs may arise due to the different assumptions of the two test designs, rather than a difference in observer behaviour. We predict that copying will be stronger using ‘no pre-test’ designs when studies compare observed preferences to predicted values. This is because the common default assumption of random choice will be incorrect if the two mate options differ even slightly in attractiveness. This would underestimate the true preference for the most attractive of the pair in the absence of social information, thus overestimating the difference in preferences between control and social treatments.

Model pairing. This category distinguishes between studies in which demonstrators are placed with an individual by the experimenters (‘forced choice’), compared to studies in which demonstrators were genuinely able to choose between potential mates prior to the demonstration period (‘actual choice’). We predicted that copying should be strongest in the actual choice category, because demonstrators here may exhibit subtle, additional behavioural signals of preference which are absent in the forced choice category.

Demonstrator behaviour. This category compared how the demonstrator interacts with the stimulus mate: is actual mating allowed to take place, or do individuals just affiliate with each other? Intuitively, observing mating rather than affiliation should provide a stronger social

signal of the demonstrator's interest in mating, and so we predicted this should lead to stronger copying.

Preference measure. How is the observer preference measured? The type of measurement has the potential to influence the strength of mating preferences for two reasons (Rosenthal, 2017; Dougherty, 2020). First, the measurement of choice may influence how observers behave during tests. For example, recording mating outcomes could result in weaker preferences compared to a proxy behavioural measure such as affiliation, because mating requires an interaction between the sexes, or because affiliation can be confounded by the time spent assessing partners (Rosenthal, 2017). Second, preference measures differ statistically in ways that could influence the observed effect size. For example, studies differ in whether preference is determined using some continuous measure such as association time, or a dichotomous measure of choice. If binary choice measures are derived from some continuous measure, then this conversion could potentially mask variation, or over-estimate preference differences because even small differences in preference are converted into an all-or-nothing response (Dougherty, 2020). This could be especially problematic when choice is based on a simple majority (over 50%) criteria, as this may often be reached by chance. Conversely, studies that record the frequency of choice reversals may underestimate preference differences, because choice reversal is such a strict criteria: the observer needs to have an initial preference for one target which is then reversed following observation.

Phylogeny

Our sample included species distributed across several taxonomic groups, as well as some genera with multiple species represented (e.g. Poeciliidae). Therefore, we needed to control for non-independence associated with shared evolutionary history by obtaining a phylogeny

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for the species sampled (Koricheva *et al.*, 2013). As no single phylogeny was available which contained all of the species in our sample, we created a supertree combining phylogenetic and taxonomic information (Nakagawa & Santos, 2012). We created the tree using the R Open Tree of Life package v3.0.9 (Michonneau *et al.*, 2016), with the positions of the genera *Poecilia*, *Gambusia* and *Limia* additionally determined using published phylogenies by Scharf *et al.* (1995), Ptacek and Breden (1998) and Reznick *et al.* (2017), respectively. As accurate branch lengths could not be obtained for the tree, branch lengths were initially set at 1. The tree was then made ultrametric, and branch lengths estimated, using Grafen's method (Grafen, 1989), and the R package Analysis of Phylogenetics and Evolution v 5.1 (Paradis *et al.*, 2004). The final phylogenetic tree is shown in figure 2.

[Fig 2 here]

Statistical analysis

All analyses were performed in R version 3.5 (R Development Core Team, 2018). For meta-analysis we used the package Metafor v2.0 (Viechtbauer, 2010). We ran multilevel meta-analysis models using the `rma.mv` function, incorporating study identity, species, phylogeny (using the tree above), and observation ID as random factors. Study identity and species were included as we extracted multiple effect sizes per study, and collected data from more than one study for 8 species. Phylogeny was incorporated into all models using a variance-covariance matrix. Meta-analysis models require that observation ID be added as a random effect in order to estimate residual error.

We first calculated the overall mean effect size by running a model with just the four random factors listing above. We considered an effect size to significantly differ from zero when the

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95% confidence intervals do not overlap zero. In order to compare our results to those of Jones & DuVal (2019), we converted our effect size into the odds ratio following Borenstein *et al.* (2009). We calculated the level of heterogeneity across all effect sizes using the I^2 statistic (Higgins *et al.*, 2003). We also partitioned heterogeneity with respect to each of the four random factors, using the method of Nakagawa & Santos (2012). I^2 values of 25, 50 and 75% are considered low, medium and high respectively (Higgins *et al.*, 2003).

To examine the effect of our moderator variables on the mean effect size, we ran mixed-effects multilevel meta-analytic models (also referred to as meta-regressions; Nakagawa & Santos, 2012). Each model included study identity, species, phylogeny and observation ID as random factors as before, but now also included one of the nine categorical moderator variables as a fixed effect. We note that this approach could potentially increase the chances of obtaining false positive results due to multiple testing. However, combining all of these fixed factors into a single model could potentially obscure significant effects, due to the modest sample size and potential collinearity among factors. We therefore take the former approach, and emphasise that statistically-significant effects should be interpreted with caution. We used the Q_M statistic to determine whether the mean effect size differed significantly across the different moderator categories (Koricheva *et al.*, 2013). We also ran intercept-only mixed-effects models for each moderator variable separately, in order to obtain estimates of the mean effect size for each categorical factor level. For one of the categorical moderators, multiple mating rate, we obtained data for 20 out of 23 species, and so tested this fixed effect using a slightly reduced dataset (149 effect sizes). This also required the creation of a pruned tree with the three unclassified species removed.

We searched for signs of publication bias in our dataset in several ways. First, we searched

for changes in the average effect size over time. Effect sizes in ecology and evolution often decrease over time, an effect which is likely driven by publication practices: the earliest studies on a given topic tend to have large effects, and weak or non-significant results may often take longer to be published (Jennions & Møller, 2002). To examine this, we ran a meta-regression with study year as a fixed effect, again with study identity, species and phylogeny as random effects. We examined the effect of study year on effect size using the Q_M statistic as described above. Second, we searched for signs of funnel plot asymmetry using two methods: Egger's test (Egger *et al.*, 1997) and trim-and-fill (Duval & Tweedie, 2000). Asymmetry tests assume that effect sizes should be distributed randomly around the mean effect size; therefore, any deviation from symmetry could suggest some effect sizes are less likely to be published than others, especially when potential 'missing' effect sizes are of low precision and magnitude (a 'small study effect': Koricheva *et al.*, 2013). Egger's test is a regression of effect size against study precision, with asymmetry indicated by a slope that differs from zero. The trim-and-fill method imputes 'missing' effect sizes in order to make the funnel plot asymmetric. However, asymmetry tests are not appropriate when effect sizes are not independent, and it has been suggested that meta-analytic residuals are more appropriate (Nakagawa & Santos, 2012). We therefore obtained meta-analytic residuals using the MCMCglmm v2.25 package (Hadfield, 2010). MCMCglmm models used the same model structure as above (study ID, species, phylogeny and observation ID as random factors), and were run using an inverse-Wishart prior for all random effects, with models run for 300,000 iterations, a thinning interval of 50 and a burn-in period of 200,000 iterations. We performed both asymmetry tests using the residuals. However, we note here that asymmetry tests are expected to be less reliable when there are potential systematic causes of heterogeneity in the dataset other than publication bias, as the assumption of a single underlying distribution of

effect sizes is clearly false (Koricheva et al., 2013). As such, results of these tests should be interpreted with caution.

Results

The final dataset included 158 effect sizes from 58 studies and 23 species, across four taxonomic groups (Figure 2). The number of effect sizes per study ranged from one to 13, with an average of 2.8. Some species were very commonly studied; 61% of effect sizes came from the three most commonly studied species: the guppy *P. reticulata*, the sailfin molly *P. latipinna*, and the fruit fly *D. melanogaster* (Figure 3). We obtained 149 effect sizes (from 22 species) testing female copying, and 14 effect sizes (from 9 species) testing male copying (Figure 3). In almost all cases (eight out of nine species), our estimates of copying in males came from species for which we also had an estimate of copying for females.

[Fig 3 here]

Across all species, observation of a positive sexual interaction resulted in a significantly increased mating preference for the target individual or phenotype, thus providing strong evidence for positive mate-choice copying (Mean= 0.58, 95% confidence interval= 0.34 - 0.83; Figure 4). This difference corresponds to an odd ratio of 2.83 (95% CI= 1.85- 4.35). Few studies found evidence for avoidance of potential mates after observation of a positive sexual interaction between a target and a rival (only 24 negative effect sizes). The total amount of heterogeneity across effect sizes (I^2) was high, at 84.82% (Figure 4). Partitioning heterogeneity among the three random factors indicated that most of the variance was at the observation level: 16.7% of heterogeneity was attributable to between-study differences, 0%

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to between-species differences, 5.6% to phylogenetic history, and 62.47% to observation-level differences.

[Fig 4 here]

The degree of mate-choice copying was significantly influenced by the taxonomic group of the study species and the type of experimental design (Table 1). In terms of taxonomic group, mammals appear to copy to the greatest extent, followed by fishes and birds, and then arthropods (Table S4; Figure 5). In terms of design type, studies using a before-and-after design detected more copying than studies with no pre-test (Table S4; Figure 5). The remaining seven categorical moderators did not significantly influence the degree of copying (Table 1; Table S4).

[Table 1 here]

[Fig 5 here]

There was no significant relationship between study year and effect size (Figure S1).

Therefore there is no evidence for significant publication bias against low-powered, non-significant results when the research field was young. There were some signs of funnel plot asymmetry: trim-and-fill analysis (using residual effect sizes) detected 28 ‘missing’ effect sizes, however all are positive and greater than the mean (Figure 6). This is likely driven by the large number of effect sizes close to zero, and to the left of the overall mean estimate (Figure 4). Therefore inclusion of these effect sizes increases the average effect size. The relationship between residual effect size and study precision was significantly negative (Egger’s regression: $F_{1, 156} = 7.66$, $P = 0.006$, $\beta = -0.13$; Figure S2), though it is unclear if this

is driven by missing effect sizes of small effect and low power (which would be suggestive of publication bias), or of large effect and high power (as found by the trim-and-fill method).

[Fig 6 here]

Discussion

We performed a meta-analysis of 158 effect sizes from 58 published studies of mate-choice copying in non-human animals. Overall, we find strong evidence that animals copy the mating preferences of others. The overall standardised mean difference was 0.57 (95% CI= 0.34- 0.81), which is considered a medium effect (Cohen, 1992). This converts to a mean odds ratio of 2.83, so that the observers in this sample are almost 3 times as likely to choose a partner or phenotype that they previously observed in a positive sexual interaction with a rival, compared to individuals with no social information. This result suggests that social information can have a significant influence on animal mating preferences across a wide range of species. Further, the strength of copying observed is similar to that reported in the recent meta-analysis of female copying by Jones & DuVal (2019: a mean odds ratio of 2.71), of which our dataset overlaps. We also detected significant variation in the degree of copying across species, which was partly explained by taxonomic group: copying was strongest for mammals, and weakest for arthropods. The strength of copying was also influenced by the type of experiment used to test for copying: copying was stronger when studies compared mating behaviour before and after the presentation of social information, in contrast to studies in which separate control and social treatment groups were compared. Interestingly, we did not detect any difference in copying between males and females, or in relation to the rate of multiple mating. We also detected little evidence for publication bias against non-significant

results.

While evidence suggests that mate-choice copying is taxonomically widespread, a small number of model species are over-represented in our dataset, and in the literature more generally: of the 89 studies identified in our search, 20 focus on guppies, nine on Japanese quail and nine on *D. melanogaster*. Despite this, species identity explained a small proportion of the variation in effect size in our analysis. This confirms that copying is not driven by a few influential species, and that within-species variability in effect size is high. Phylogenetic history explained only a small amount of variation in effect sizes, indicating that any similarities between species are not due to them being closely related evolutionarily. This is unsurprising, given the large evolutionary distances between the species in the dataset (with the exception of species in the Poeciliidae), and the evolutionary lability of behavioural traits (Blomberg *et al.*, 2003). Nevertheless, we did detect differences in the degree of copying when we sorted the species in our dataset into four broad taxonomic groups: mammals, birds, fishes, and arthropods (incorporating insects, arachnids and crustaceans). The degree of copying was highest for mammals, followed by birds and fishes, and then lowest for arthropods. This finding could be explained by broad-scale differences in cognitive ability, ecological conditions or social group size. However, these results should be interpreted with caution: firstly because the number of effect sizes for mammals and arthropods was small, and secondly because the small number of species tested across the entire dataset means it is unclear how generalizable these results are. Importantly, we need more tests of copying in species groups other than those highlighted here. For example, to our knowledge there have been no experimental tests of copying in amphibians, reptiles, or non-human primates.

We found that the type of experimental design significantly influenced the degree of copying.

Copying was stronger for studies with a ‘before-and-after’ design, compared to studies with separate control and social treatment groups (no pre-test). This is the opposite of what we predicted, based on our hypothesis that no pre-test studies may often underestimate preferences in the absence of social information. We note however that our categories of ‘before-and-after’ and ‘no pre-test’ designs mostly align with the ‘random’ and ‘unattractive’ categories used by Jones and Duval (2019), which relate to whether the study used a reversal paradigm to test for copying (the unattractive category). The alignment comes from the fact that the reversal paradigm is a subset of the ‘before-and-after’ test. Accordingly, Jones and DuVal (2019) found that copying was stronger when using a reversal paradigm, which is consistent with our result shown here. One potential explanation for the observed effect could be related to the fact that before-and-after designs test each individual twice, potentially in quick succession. This provides the opportunity for observers to gain experience that could influence their choice in a non-random way. For example, individuals may become choosier with successive encounters because they have more information on the quality of mates in the population, they perceive mate density to be higher, or because they are attempting to ‘trade-up’ from previous mates (e.g. Pitcher *et al.*, 2003).

There were also a range of moderators which did not significantly influence the degree of copying. For example, copying was performed to a similar extent in animals born in the wild or in captivity. This firstly confirms that mate-choice copying is not an artefact of captivity – it is a real behaviour which exists in wild populations. However, the recent meta-analysis by Jones & DuVal (2019) found that females copied more when tested in the wild compared to when tested in captivity. This discrepancy likely arises because our moderator focuses on observer history prior to, but not during, the behavioural tests, and suggests that the environment during the test is more important for influencing copying behaviour. Copying

was not influenced by the mating rate of the species tested. This null result could be explained partly by the lack of data on species with low rates of multiple mating, and we suggest more studies should be carried out on such species. Importantly, any conclusions relating to this moderator may also be further limited by the fact that species with low rates of multiple mating are taxonomically limited in our sample, occurring only in birds and arthropods. Nevertheless, mate-choice copying has been shown in at least two bird species that show some form of social monogamy and biparental care (zebra finches and Japanese quail), even though theory suggests that copying should not be favoured because of the diminishing returns associated with sharing a mate that provides direct benefits or parental care (Vakirtzis and Roberts, 2009). We also found no difference in the strength of generalised versus individual copying. These two forms of copying may require different cognitive abilities, but whether this leads to differences in the strength of copying is not clear. Crucially, the relative prevalence, and strength, of these two forms of copying has important evolutionary consequences. Both forms of copying can widen the gap between attractive and unattractive males (Leadbeater, 2009), create frequency-dependent bias in mate choice (Santos *et al.*, 2014) and support the invasion of new traits into a population (Santos *et al.*, 2017). However, because generalised copying allows learned preferences to be applied to multiple mates, it can lead to the cultural transmission of preferences, and so has the potential to be a much stronger evolutionary force than individual copying.

Most surprisingly, we found no evidence that males copy less than females. This result is unexpected as males may be substantially increasing their exposure to sperm competition by copying the mate choices of their rivals (Simmons, 2001; Vakirtzis and Roberts, 2009). In support of this, there is widespread evidence that males often prefer to mate with virgin females if given the choice (Simmons, 2001; Bonduriansky, 2001). Again, this could be

partly explained by the relatively small number of studies testing male copying. Another possibility is that when faced with previously-mated females, males may ejaculate more sperm as a defence against combat sperm competition, instead of rejecting a mating opportunity (Simmons, 2001; Kelly & Jennions, 2011). The ability of males to strategically allocate sperm in this way has the potential to reduce the costs of copying a rival's choice. Copying could also be beneficial to males if they can reduce the risk of being copied themselves, perhaps by mating or courting out of view of rival males (Simmons, 2001; Brown *et al.*, 2012; le Roux *et al.*, 2013), or by mating with less-preferred females when rivals are present as a form of deception (also known as the 'audience effect': Plath *et al.*, 2008; Castellano *et al.*, 2016; Witte *et al.*, 2018). Alternatively, male mate-choice copying may be likely when males face high costs of reproduction, as appears to be the case for the fantail darter *Etheostoma flabellare*, the three-spined stickleback *Gasterosteus aculeatus*, and the broadnosed pipefish *Syngnathus typhle* (Witte *et al.*, 2015). Indeed, mate-choice copying studies have often been performed using species with paternal care (fish, zebra finches), and therefore high male reproductive investment. It will therefore be useful to test for copying in species which exhibit a broader range of mating systems and reproductive strategies than that shown by the current available sample.

Several other aspects of experimental design did not influence the degree of mate choice copying. For example, copying was observed regardless of the type of social information available to the observer (whether the demonstrator mated, courted, avoided or affiliated with a partner), how the observer preference was measured, or whether the demonstrator was allowed to 'choose' a target individual or was artificially placed with one. Nevertheless, variation in other aspects of experimental design do have the potential to contribute to some of the unexplained variability in effect sizes seen across studies. For example, for indirect

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measures of mate choice (Rosenthal, 2017), the criteria used to determine mating preferences differs between studies. Vukomanovic and Rodd (2007) conducted mate-choice copying experiments with the sailfin molly *Poecilia latipinna* using different criteria to investigate how this could influence the measurement of copying. Using the criteria of Dugatkin (1992), where females had to spend over 50% of their time within a 13cm “preference zone” in front of the male, significant copying was detected. However, using the criteria of Lafleur *et al.* (1997), where females had to spend 15 consecutive seconds in a 2.5cm preference zone, no copying was detected. This demonstrates that even when recording the same behaviours, results can differ depending on exactly which methodology is used.

Though several moderators did influence the strength of copying in our sample, most of the heterogeneity in effect size detected (both here and in Jones & DuVal, 2019) remains unexplained. This suggests there are other factors which influence the degree of copying which we were unable to include in our meta-analysis. In many cases this is because of the difficulty associated with obtaining good estimates across all species sampled. For example, a potentially important driver of copying, and mate choice in general, is the cost of mate sampling. However we have very few estimates of the costs of mate sampling and mate choice in any species, so that broad-scale comparisons are difficult (Rosenthal, 2017). Interestingly, empirical studies that have attempted to indirectly measure this effect, by testing copying in high-cost environments, have failed to find any significant change in copying (Briggs *et al.*, 1996; Dugatkin & Godin, 1998). Another key driver of copying is expected to be the ability to assess mate quality, which again will be difficult to accurately estimate for all species. However, empirical tests have found some support for this effect: for example, copying is more likely when mates are more similar in guppies and mollies (Dugatkin, 1996; Witte & Ryan, 1998). Related to this, a valuable topic for future research

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would be the nature of memory in the context of mate-choice copying. How long are demonstrations remembered for? How easily are these memories forgotten or overwritten with conflicting experiences?

In summary, this meta-analysis of 58 experimental studies suggests that mate-choice copying is a widespread and robust phenomenon across the animal kingdom. Despite different methodological approaches, the average effect size is very similar to that found in the recent meta-analysis of mate-choice copying by Jones & DuVal (2019), of which our dataset overlaps. We found evidence that the amount of copying differs significantly across taxonomic groups and between the two main types of experimental design found in the literature, but no evidence that copying is influenced by sex or the rate of multiple mating. Importantly, our systematic review has also revealed areas where more empirical work is needed. Unfortunately, though mate-choice copying has been observed across a wide taxonomic range, most studies are still only performed on a few model species. In addition to uncovering the details of how mate-choice copying operates within a species, time should be taken to investigate how widespread the phenomenon is across the animal kingdom, and which aspects of a species' ecology or biology predispose the evolution of copying.

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Table 1. Results of meta-regression models testing the effecting of ten moderators on the strength of copying. The effect of each factor was tested using a mixed-effects model, with study ID, species, phylogeny and observation ID as random factors, and one of the ten moderators as a fixed factor. Significance was determined using the Q_M statistic. All moderators were tested using the full dataset (158 effect sizes), with the exception of the rate of multiple mating, which was tested using a reduced dataset (149 effect sizes). Significant moderators are highlighted in bold.

Moderator	Q_M	P
Taxonomic group	8.57	0.04
Choosing sex	0.05	0.82
Rate of multiple mating	0.15	0.70
Animal birth location	1.25	0.53
Generalised or individual copying	0.57	0.45
Design type	6.11	0.01
Model pairing	0.01	0.92
Demonstrator behaviour	2.00	0.57
Preference measure	6.37	0.27
Study year	1.97	0.16

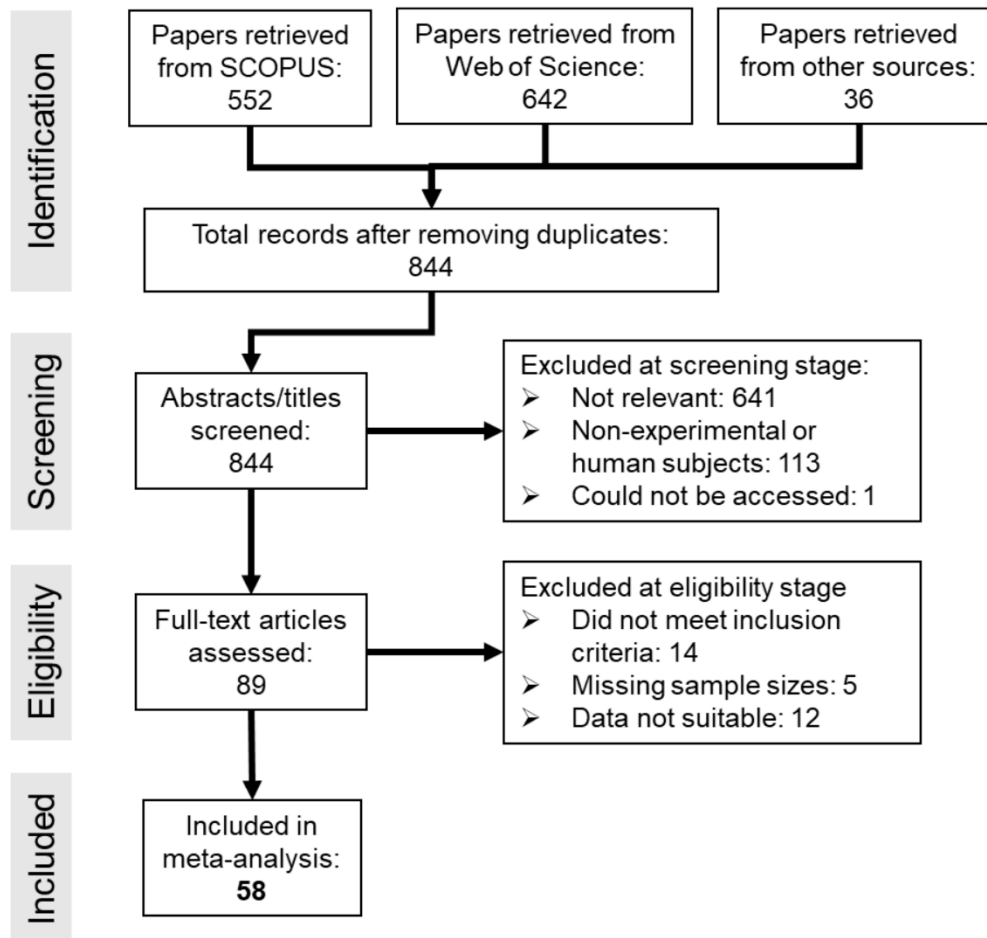


Figure 1. PRISMA diagram showing the literature search process.

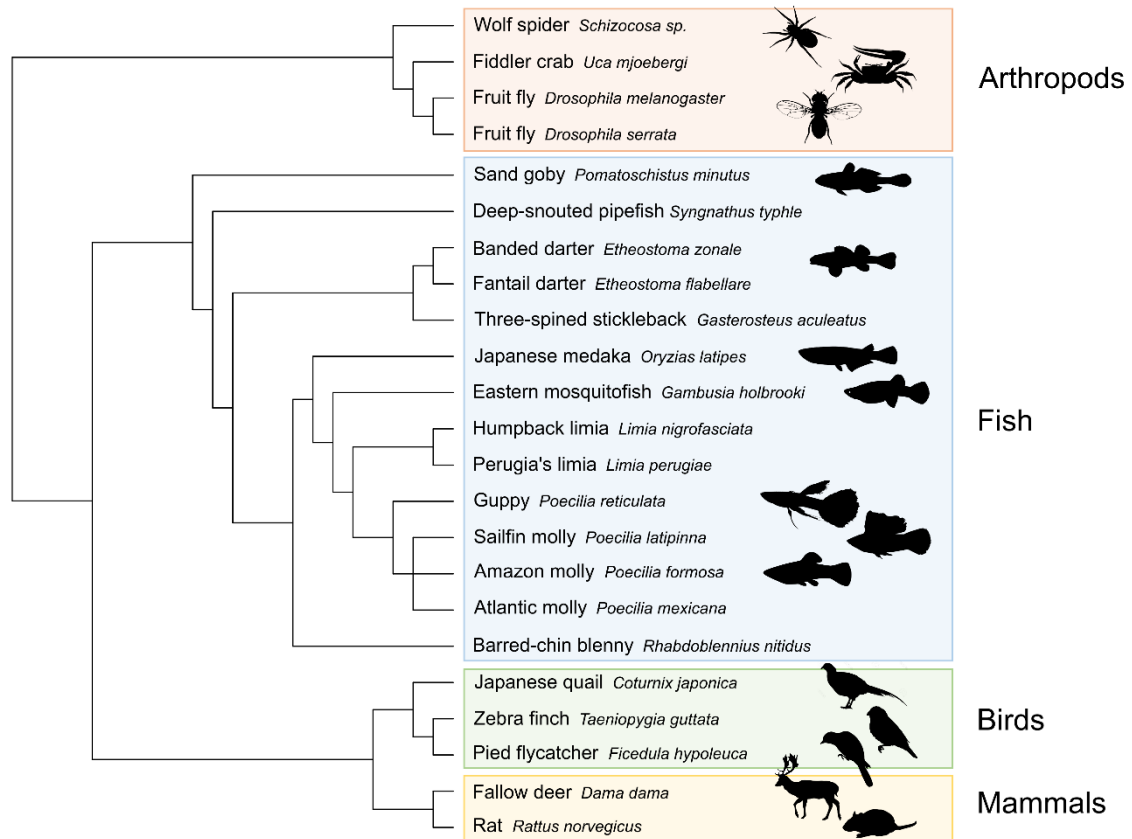


Figure 2. The full phylogenetic tree used in the meta-analysis, with taxonomic groups highlighted. Note that the arthropod category includes arachnid, crustacean and insect species.

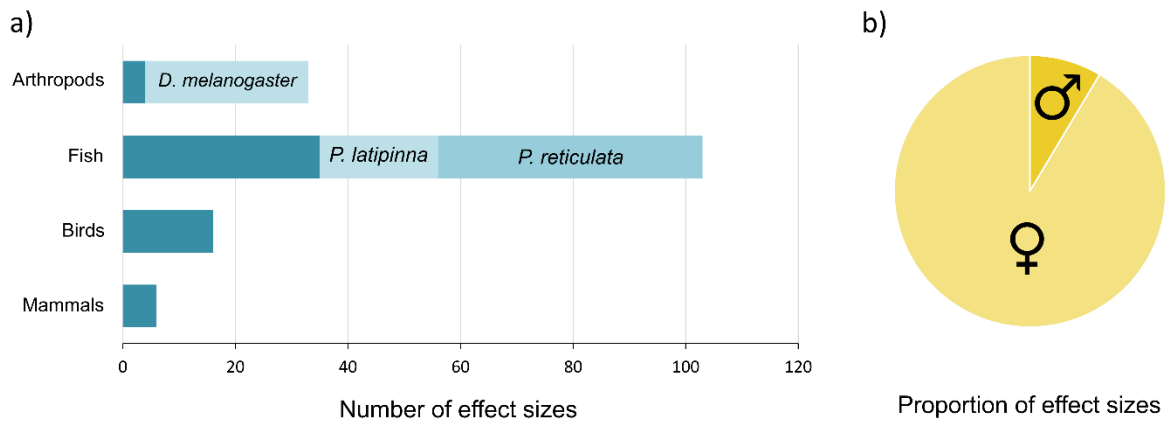


Figure 3. The number of effect sizes in the analysis in relation to: a) the four taxonomic groups, and b) the two sexes. In panel a), the different colours show the number of effect sizes for the three most commonly-studied species (*Poecilia reticulata*, *Drosophila melanogaster*, and *Poecilia latipinna*), which together account for 61% of all effect sizes in the analysis.

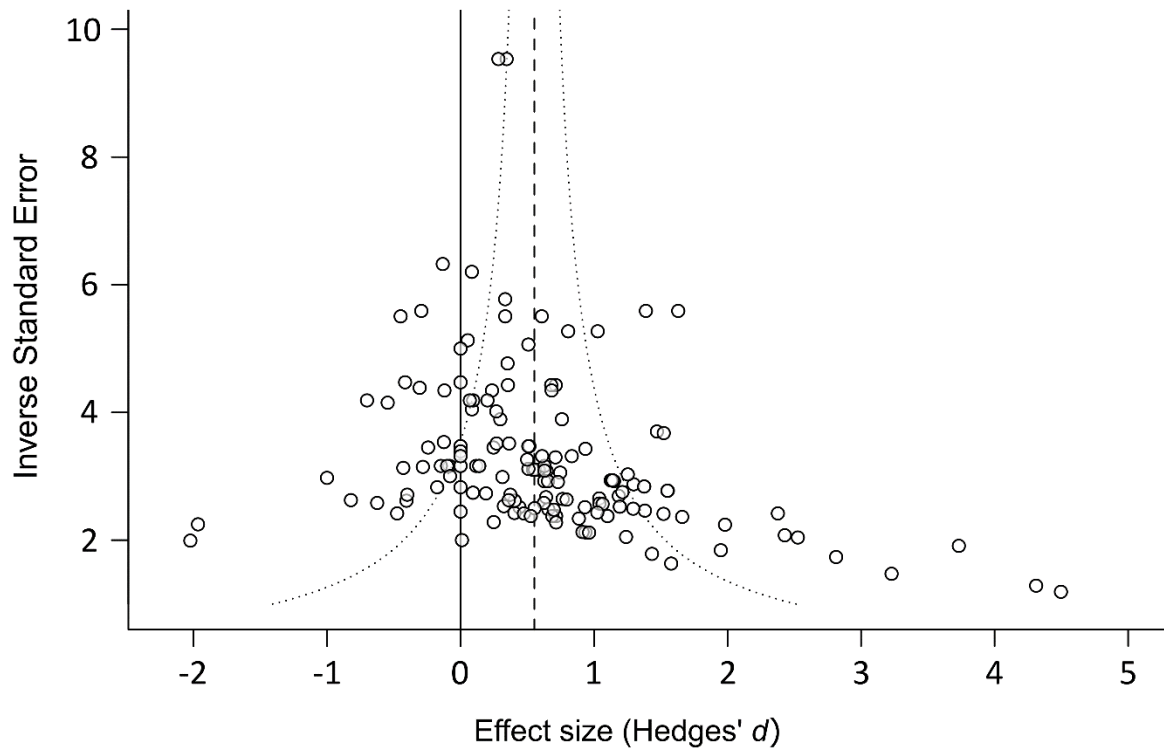


Figure 4: Funnel plot showing the relationship between inverse standard error (precision) and effect size (the standardised mean difference, Hedges' d). The dashed vertical line indicates the mean effect size from a random-effects-only model (0.57).

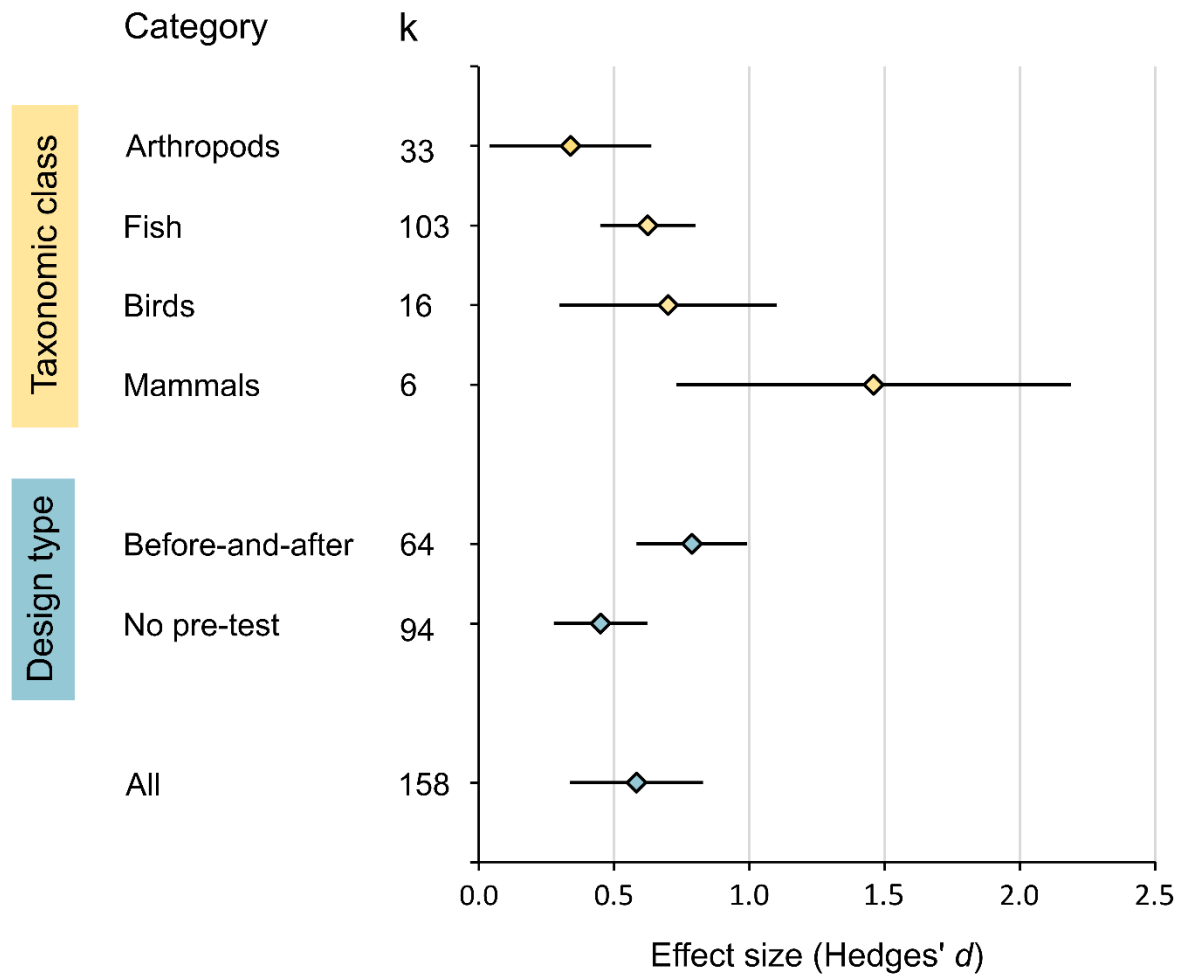


Figure 5. Forest plot showing the mean effect size (the standardised mean difference, Hedges' *d*) for each factor level for two moderators: taxonomic class (yellow diamonds) and design type (blue diamonds). The mean effect size for the whole dataset is shown in black for comparison. See text for details on the two moderators. Bars indicate 95% confidence intervals. *k*= the number of effect sizes for each factor level.

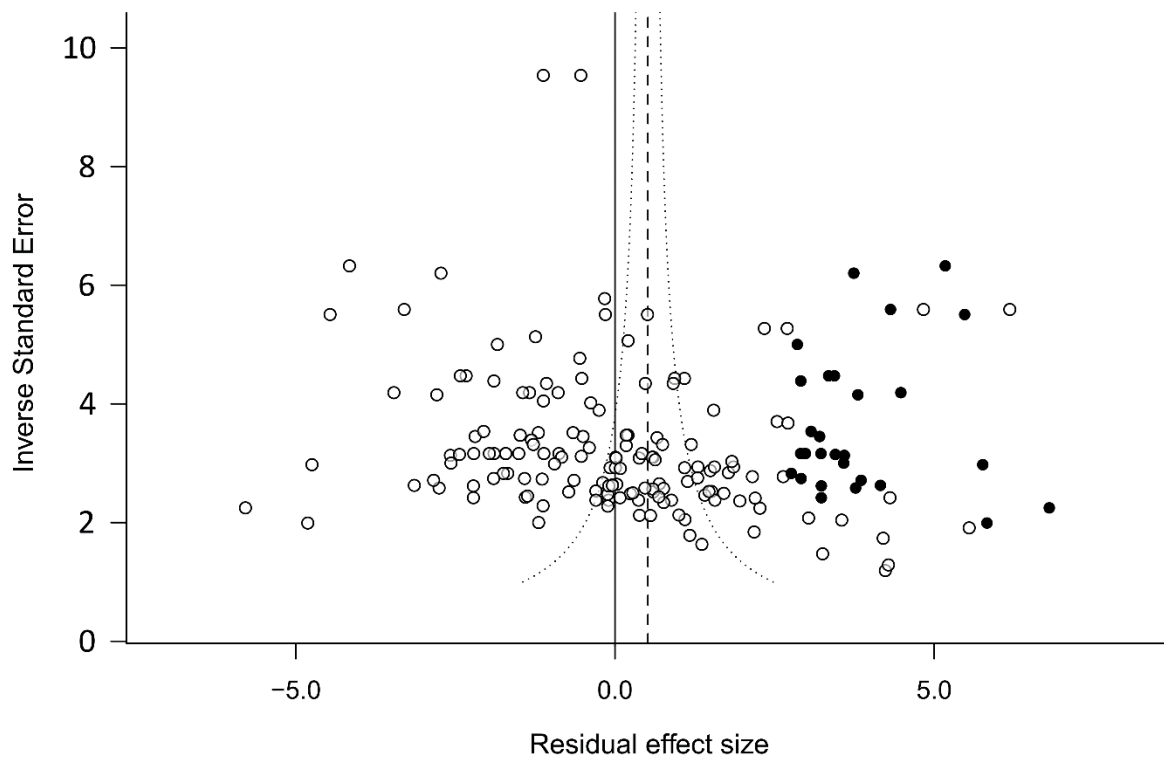


Figure 6. The results of a trim-and-fill analysis testing for funnel plot asymmetry, with residual effect size plotted against inverse standard error (larger values represent more reliable estimates). The true effect sizes are in white, and the 28 ‘missing’ effect sizes are in black. The dashed vertical line shows the new mean effect size on the residual scale, estimated after adding the 28 ‘missing effect sizes’ to the model.

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Supplementary methods and results for:

Davies, AD¹, Lewis, Z² & Dougherty, LR^{1*} 2020. A meta-analysis of factors influencing the strength of mate choice copying in animals. *Behavioral Ecology*.

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Table S1: Reasons for rejecting papers that were read in full.

Study	Species	Explanation
Alonzo, 2008	<i>Symphodus ocellatus</i>	Missing sample sizes
Amlacher and Dugatkin, 2005	<i>Poecilia reticulata</i>	No control data
Bailey and Zuk, 2009	<i>Teleogryllus oceanicus</i>	Not mate choice copying
Bierbach <i>et al.</i> , 2013a	<i>Poecilia mexicana</i>	Statistics not appropriate
Bierbach <i>et al.</i> , 2011	<i>Poecilia mexicana</i>	Statistics not appropriate
Bierbach <i>et al.</i> , 2013b	Several	Not mate choice copying
Castellano <i>et al.</i> , 2016	N/A	Model: no data
Dugatkin, 1992	<i>Poecilia reticulata</i>	Statistics not appropriate
Dugatkin, 1996	<i>Poecilia reticulata</i>	Statistics not appropriate
Dugatkin, 2007	<i>Poecilia reticulata</i>	Statistics not appropriate
Dugatkin and Druen, 2007	<i>Poecilia reticulata</i>	Statistics not appropriate
Dugatkin <i>et al.</i> , 2002	<i>Poecilia reticulata</i>	Not mate choice copying
Fiske <i>et al.</i> , 1996	<i>Gallinago media</i>	Observational study
Freed-Brown and White, 2009	<i>Molothrus ater</i>	Missing sample sizes
Godin <i>et al.</i> , 2005	<i>Poecilia reticulata</i>	Statistics not appropriate
Goncalves <i>et al.</i> , 2003	<i>Salaria pavo</i>	Not mate choice copying
Goulet and Goulet, 2006	<i>Amblyglyphidodon leucogaster</i>	Observational study
Höglund <i>et al.</i> , 1995	<i>Tatrao tetrix</i>	Missing sample sizes
Kavaliers <i>et al.</i> , 2006	<i>Mus musculus</i>	Indirect social information

Kniel <i>et al.</i> , 2015a	<i>Taeniopygia guttata</i>	Statistics not appropriate
Kniel <i>et al.</i> , 2015b	<i>Taeniopygia guttata</i>	Statistics not appropriate
Kniel <i>et al.</i> , 2017	<i>Taeniopygia guttata</i>	Statistics not appropriate
Makowicz <i>et al.</i> , 2010	<i>Poecilia reticulata</i>	No control data
Monier <i>et al.</i> , 2018	<i>Drosophila melanogaster</i>	Statistics not appropriate
Monier <i>et al.</i> , 2019	<i>Drosophila melanogaster</i>	Not mate choice copying
Ohlyan <i>et al.</i> , 2012	<i>Poecilia reticulata</i>	Missing sample sizes
Persaud and Galef, 2005	<i>Coturnix japonica</i>	Not mate choice copying
Reynolds and Jones, 1999	<i>Pomatoschistus microps</i>	Not mate choice copying
Sakaluk and Ivy, 1999	<i>Cyphoderris strepitans</i>	Not mate choice copying
Witte and Ryan, 2002	<i>Poecilia latipinna</i>	Missing sample sizes
Witte <i>et al.</i> , 2018	<i>Poecilia mexicana</i>	Statistics not appropriate

Table S2. Comparison of key methodological differences between the current study and the recent meta-analysis of mate-choice copying by Jones & DuVal (2019: see text for reference).

Stage	Methodology	Jones & DuVal, 2019	Davies et al, 2020
Literature search	Search date	May 2019	April 2019
	Sources	Web of Science	Web of Science, Scopus, Studies cited by and citing Vakirtzis (2011)
	Articles screened	365	844
	Number of assessors	1	1
Study selection	Humans	No	No
	Sex	Females	Females and males
	Control group	Not required	Not required
	Copying type	Individual and generalised	Individual and generalised
	Articles assessed	91	89
Data extraction	Effect size	Odds ratio	Standardised mean difference (Hedges' d)
	Data type	Dichotomous	Dichotomous, continuous
	Re-analyses?	No	Yes
	Contacting authors?	No	Yes
	Directionless effect sizes?	Excluded	Included
Sample sizes	Included studies	40	58
	Included species	17	23
	Included effect sizes	103	158
Analyses	Approach	Bayesian	Restricted maximum likelihood
	Package	MCMCglmm	Metafor
	Random effects	Study ID, species, phylogeny, observation	Study ID, species, phylogeny, observation
	Heterogeneity	I^2	I^2
	Meta-regressions	Single model (4 moderators)	Separate models (9 moderators)
Publication bias	Temporal trends	None	Meta-regression
	Asymmetry	Modified trim-and-fill (residuals) Modified Egger's regression (residuals)	Modified trim-and-fill (residuals) Modified Egger's regression (residuals)

Table S3: Sources used to classify species according to their rate of multiple mating within a breeding season. Where possible we used paternity data or quantitative measurements of mating rates.

Taxonomic group	Latin name	Multiple mating rate	Source	Evidence
Arthropod	<i>Drosophila melanogaster</i>	High	Imhof et al., 2002	Paternity data
	<i>Drosophila serrata</i>	High	Frentiu et al., 2008	Paternity data
	<i>Schizocosa sp.</i>	Low	Norton & Uetz, 2005	Mating observations
	<i>Uca mjoebergi</i>	Low	Vega-Trejo & Backwell, 2017	Descriptive: "Wandering females approach and briefly enter the burrows of one or more courting males before choosing a mate by remaining in a breeding burrow..." pp 170
Fish	<i>Etheostoma flabellare</i>	High	Moran et al., 2013	Descriptive: "...multiple females approach and lay eggs in the nest." pp 1258. "The females then attach their eggs in the nests of multiple males." pp 1268
	<i>Etheostoma zonale</i>	High	Moran et al., 2013	Descriptive: "...females approach males and attach eggs to nearby algae." pp 1258
	<i>Gambusia holbrooki</i>	High	Zane et al., 1999	Paternity data
	<i>Gasterosteus aculeatus</i>	High	Frommen et al., 2009	Spawning observations
	<i>Limia nigrofasciata</i>	Unknown	NA	NA
	<i>Limia perugiae</i>	High	Schartl et al., 1993	Paternity data
	<i>Oryzias latipes</i>	High	Weir & Grant, 2010	Spawning observations

	<i>Poecilia formosa</i>	N/A	Hubbs & Hubbs, 1932	Parthenogenetic
	<i>Poecilia latipinna</i>	High	Travis <i>et al.</i> , 1990	Paternity data
	<i>Poecilia mexicana</i>	Unknown	NA	NA
	<i>Poecilia reticulata</i>	High	Houde, 1997	Paternity data
	<i>Pomatoschistus minutus</i>	High	Forsgren <i>et al.</i> , 2006	Spawning observations
	<i>Rhabdoblennius nitidus</i>	High	Miyano <i>et al.</i> , 2006	Spawning observations
	<i>Syngnathus typhle</i>	High	Jones <i>et al.</i> , 1999	Paternity data
Bird	<i>Coturnix japonica</i>	Low	Nichols, 1991	Pairing observations
	<i>Ficedula hypoleuca</i>	Low	Lundberg & Alatalo, 1992	Paternity data
	<i>Taeniopygia guttata</i>	Low	Birkhead <i>et al.</i> , 1990	Paternity data
Mammal	<i>Dama dama</i>	High	Apollonio <i>et al.</i> , 1992	Mating observations
	<i>Rattus norvegicus</i>	High	Glass <i>et al.</i> , 2016	Paternity data

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Table S4: Mean effect size (Hedges' *d*) estimates for all moderator levels from the nine meta-regression models.

Moderator	Category	n effect sizes	n studies	n species	Mean <i>d</i>	Lower 95% CI	Upper 95% CI
NA	All	158	58	23	0.583	0.338	0.829
Taxonomic group	Arthropods	33	10	4	0.339	0.040	0.638
	Birds	16	11	3	0.700	0.298	1.101
	Fish	103	34	14	0.625	0.448	0.801
	Mammals	6	3	2	1.459	0.730	2.188
Rate of multiple mating	High	131	44	15	0.605	0.284	0.926
	Low	18	13	5	0.501	-0.018	1.019
Choosing sex	Female	149	50	22	0.578	0.324	0.832
	Male	14	8	9	0.629	0.163	1.095
Design type	Before-and-after	64	28	12	0.787	0.583	0.992
	No pre-test	94	30	15	0.450	0.277	0.623
Model pairing	Manipulated	149	54	22	0.587	0.338	0.837
	Natural	9	5	3	0.561	0.022	1.100
Demonstration type	Affiliation	101	37	17	0.661	0.383	0.939
	Avoidance	2	1	1	1.181	-0.035	2.397
	Courtship	9	3	3	0.708	0.085	1.331
	Mating	46	18	7	0.462	0.147	0.778
Behaviour of focal individual	Choice frequency	52	19	9	0.563	0.222	0.904
	Reversal frequency	14	9	4	0.403	-0.011	0.817

	Mating frequency	8	3	2	0.426	0.137	0.715
	Mating latency	4	1	1	0.289	-0.470	1.049
	Receptive behaviours	5	3	3	0.323	-0.327	0.974
	Affiliation time	75	39	17	0.753	0.562	0.945
Generalised or individual copying	Generalised	30	11	4	0.692	0.262	1.122
	Individual	128	49	22	0.530	0.201	0.860
Animal birth location	Captive	109	38	12	0.609	0.338	0.880
	Mixed	4	1	1	0.059	-0.922	1.039
	Wild	45	20	14	0.565	0.235	0.896

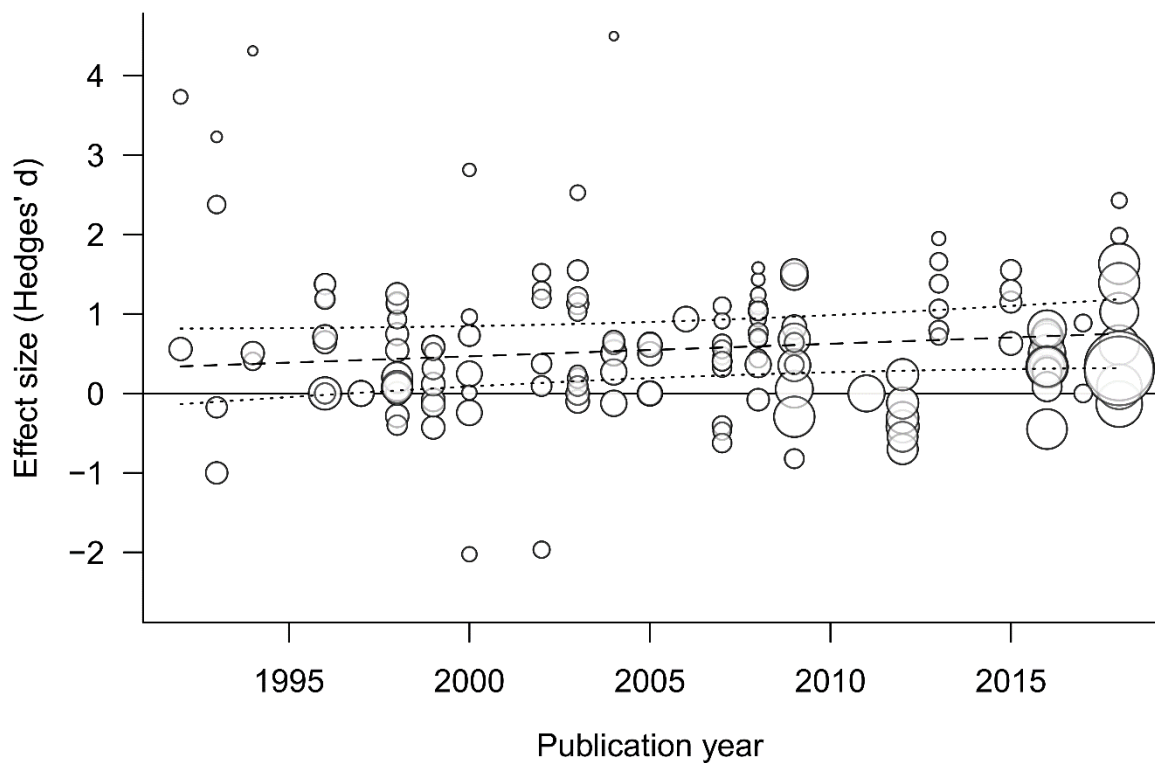


Figure S1. Bubble plot showing the relationship between effect size (Hedges' d) and study year. The dashed line represents the line of fit from a meta-regression including study year as a fixed factor and study identity, species, and phylogeny as random factors (dotted lines represent the 95% confidence interval around the fitted line). The points are scaled according to the inverse of their variance, so that larger points are given greater weight in the model, and represent more reliable estimates.

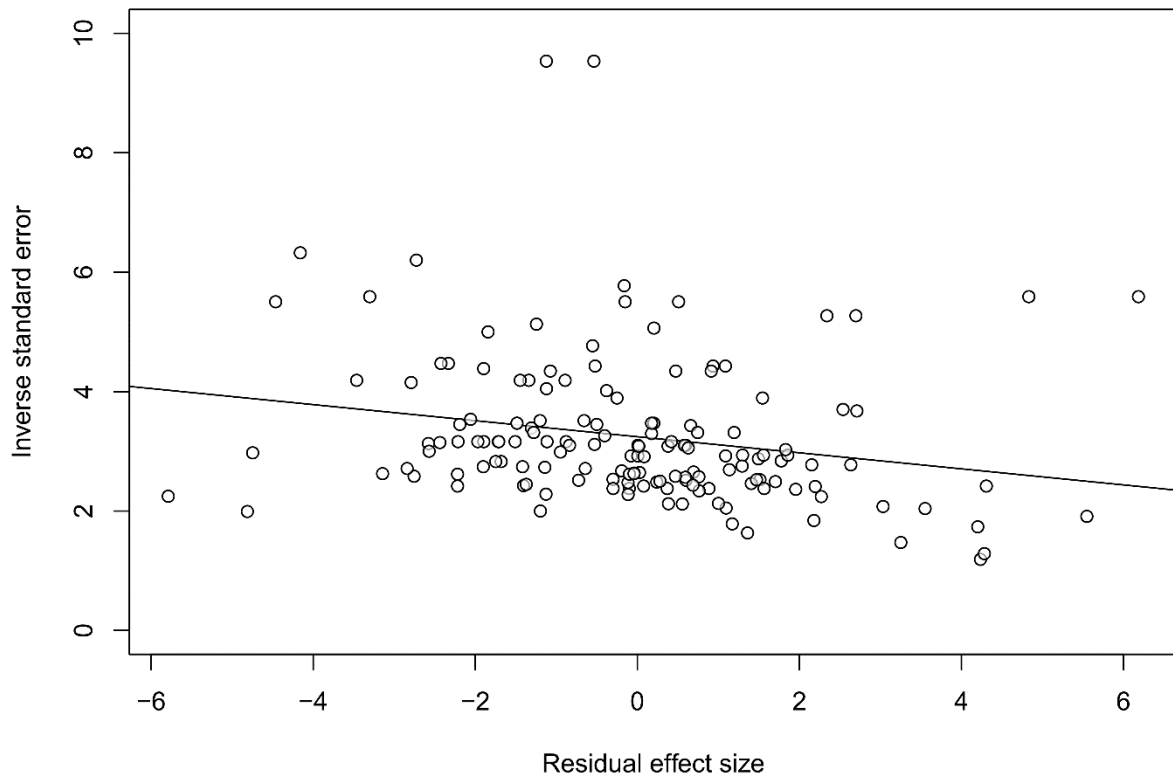


Figure S2. The relationship between residual effect size and inverse standard error (larger values represent more reliable estimates). The line shows the fitted line from a linear regression of residual effect size against inverse standard error.