

# The better, the choosier: A meta-analysis on interindividual variation of male mate choice

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## Abstract

Male mate choice occurs in several animal species, but we know little about the factors that influence the expression of this behaviour. Males vary in their capacity to acquire mates (i.e. male quality), which could be crucial to male mate choice expression but it is often overlooked. Using a meta-analytical approach, we explore interindividual variation in the expression of male mate choice by comparing the mating investment of males of different qualities and phenotypes to high- and low-quality females. We used two datasets that together contained information from 60 empirical studies, comprising 52 species. We found that males of all qualities and phenotypes prefer high-quality females, but differ in the strength of such preference. High- and medium-quality males are choosier than low-quality males. Similarly, males that are larger or in greater body condition are choosier than their counterparts. In contrast, male body mass and age are not associated with changes in male mate choice. We also show that experimental design may influence our understanding of male mating investment patterns, which may limit the generalisation of our findings. Nonetheless, we argue that male quality may be an important feature in the expression of male mate choice.

## KEYWORDS

differential resource allocation, interindividual variation, male mate choice, male mate preferences, mate availability, prudent choice

## INTRODUCTION

There is little doubt that mate choice has shaped the evolution of many species (Rosenthal, 2017), but identifying when and which individuals should be choosy can still pose a challenge. Mate choice involves not only binary decisions, such as to accept or to reject a mate, but also the amount of resources to invest in each mate before, during, and after copula (Bonduriansky, 2001; Edward, 2015; cf. Halliday, 1983). It is the relationship between the capacity to (reproductively) invest in prospective mates and mate availability that should predict the expression

of mate choice (Edward & Chapman, 2011). When there are more prospective mates than an individual can invest optimally in, that individual must make reproductive decisions that lead to mate choice. Using this rationale, it is intuitive to understand why the traditional theory of sexual selection posits that females should be selective regarding their mates: they have a limited amount of reproductive resources (eggs) and often many males willing to mate with them (Bateman, 1948; Trivers, 1972). On the other hand, male mate choice should be restricted to situations in which males have less reproductive resources (e.g. limited sperm production) or fewer mating

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opportunities (e.g. synchronised female maturation). Yet, it is unlikely that such specific situations explain all occurrences of male mate choice given that this behaviour is widespread in the animal kingdom (Bonduriansky, 2001; Edward & Chapman, 2011). It is thus imperative to explore how various factors can affect the expression of male mate choice.

Several factors beyond breeding resources are vital in explaining mate choice evolution. For instance, greater mate quality variation should increase the benefits of mate choice while greater mate encounter rate should decrease its costs (Kokko & Monaghan, 2001). However, even under optimal conditions for male mate choice evolution, male mate choice may not be viable if all males prefer the same females (the ones that provide males the most benefits, i.e. high-quality females). This is because the net benefit of being choosy decreases as competition for a subset of females increases (Servedio & Lande, 2006; see further discussion in Fitzpatrick & Servedio, 2018). However, this rationale does not account for variation in male capacity to acquire mates, such as their individual attractiveness or fighting ability. We hereby refer to this individual male capacity to acquire mates as male quality, but we note that our use of this term is not necessarily connected to individual fitness (Wilson & Nussey, 2010) or overall condition (Rowe & Houle, 1996). Several theoretical models indicate that males may express mate choice differently according to their quality (Chevalier et al., 2020; Fawcett & Johnstone, 2003; Härdling et al., 2008; Härdling & Kokko, 2005; Puurtinen & Fromhage, 2017; Venner et al., 2010). However, these studies vary in their predictions of male mate choice expression (e.g. quality variation in Fawcett & Johnstone, 2003; mating costs in Puurtinen & Fromhage, 2017) depending on which factors are used and how they model them.

While high-quality males are often predicted to prefer high-quality females, it is less clear how low-quality males should behave. First, low-quality males may also prefer high-quality females if there is a strong benefit of mating with high-quality females and if there is very weak competition for them. However, we argue that this should rarely occur, given that males commonly compete for access to females in nature (Andersson, 1994). Second, low-quality males may not show any preferences, thereby behaving opportunistically. Third, low-quality males may prefer low-quality females (assortative mate preference) to avoid wasting resources in courting and mating with females they have low chances of securing. The rationale of these predictions is that, because the net benefit of male mate choice is male quality dependent, so should be its expression. Theoretical studies with these predictions (Chevalier et al., 2020; Fawcett & Johnstone, 2003; Härdling et al., 2008; Härdling & Kokko, 2005; Puurtinen & Fromhage, 2017; Venner et al., 2010) assume males can assess their own quality innately and act accordingly, meaning that such male

mate choice dependency on male quality should occur even when males are inexperienced and in the absence of competitors.

To be able to test whether male mate choice depends on male quality, one needs to know which male traits predict male mate acquisition capacity (i.e. we need to define male quality beforehand). Yet, researchers commonly assume male quality based solely on the expression of a given male trait. For instance, under a traditional perspective of sexual selection, males that are larger, heavier, older, and have greater body condition are thought to be more attractive or better fighters in many species (Andersson, 1994) and are then assumed to be of better quality. Even if such patterns are generally valid, assuming such phenotypic patterns without prior testing could hinder broad theoretical conclusions on male mate choice patterns. For example, greater size may be detrimental to male mate acquisition instead of beneficial (e.g. Gress et al., 2013; Székely et al., 2004), and the same can be said about male age (e.g. Wilder & Rypstra, 2007). Therefore, caution is required to understand patterns of male mate choice in nature, making it important to understand the relative importance various traits have on both mate choice and how we assess male quality.

Drawing broad conclusions about mate choice can be further challenging because empirical studies are extremely diverse regarding their experimental design (reviewed in Dougherty, 2020). For example, when testing for male mate choice, researchers can allow males to interact with females in trials or control for female mating decisions using physical barriers or indirect cues (Dougherty, 2020). Moreover, researchers may also provide a single female or multiple females to males to assess male mate choice (i.e. no- vs. multiple-choice tests; Dougherty, 2020; Dougherty & Shuker, 2015). These factors potentially influence mate choice outcomes (Dougherty, 2020; Dougherty & Shuker, 2015) and thus have to be taken into consideration when examining mate choice patterns. In addition, the female traits used to elicit male mate choice often vary from study to study, and sometimes are assumed to reflect female quality without species-specific evidence. For instance, males are often predicted to prefer larger females as they should be more fecund (Bonduriansky, 2001), but fecundity is not always predicted by female size (e.g. Schneider & Elgar, 2002). This means that different female traits, and whether they truly represent female quality, possibly affect male mate choice patterns as well.

Here we conduct a meta-analysis to explore interindividual variation in male mate choice and the role that phenotypic assumptions and experimental design have on our understanding of the expression of male mate choice. To do so, we used experimental studies in which males of different phenotypes could invest resources in females of different qualities before, during, or after mating with them. Following theoretical studies

(e.g. Chevalier et al., 2020; Fawcett & Johnstone, 2003; Härdling et al., 2008; Härdling & Kokko, 2005; Puurtinen & Fromhage, 2017; Venner et al., 2010), we hypothesise that male quality influences male mate choice expression. We predict that male mate preferences vary with male quality, so that high-quality males prefer high-quality females, while low-quality males prefer low-quality females (so they do not waste resources being outcompeted by other males) or show no preferences. Our second hypothesis is that certain male phenotypes, without necessarily verifying that they truly represent male quality, can generate the same pattern of male mate choice that male quality does. We thus predict that males that are large, heavy, old, and in good body condition prefer high-quality females, while males that are small, light, young, and in low body condition prefer low-quality females or show no preferences. We also explored and verified several aspects related to experimental design and female traits used in male mate choice tests to ensure that our analyses are robust and can be generalised.

## MATERIAL AND METHODS

We followed PRISMA-EcoEvo reporting guidelines (O’Dea et al., 2021) as much as possible to conduct our meta-analysis (Figure 1, Supporting information SII). All stages of the methods (i.e. identification, screening and extraction) were conducted by P.P., which were partially checked by S.N. and M.K.

## Search protocol

As a first step in our systematic literature search, we conducted keyword searches in *ISI Web of Science* and *Scopus* databases on July 2nd, 2019. The sets of keywords we used were associated with male or mutual mate choice or preference, but they differed slightly between these databases due to the distinct Boolean characters available in each database (see Supporting information SI2). Additionally, still on July 2nd, 2019, we searched backward and forward citations of three highly relevant studies to our meta-analysis using *ISI Web of Science*: two reviews of male mate choice (Bonduriansky, 2001; Edward & Chapman, 2011) and a meta-analysis on cryptic male mate choice (Kelly & Jennions, 2011). Altogether, after removing duplicated references, we obtained 3130 studies (Figure 1).

We inspected titles and abstracts of all papers retrieved in our searches, applying our inclusion criteria (see below). We identified 95 studies as relevant to our meta-analysis after this initial screening. We then searched backward and forward citations of these selected papers on March 5th, 2021, using the application *citationchaser* (Haddaway et al., 2021), which uses *the Lens* database. Because we conducted this additional search to gather recently published studies, we only considered citations from 2018, providing 430 other published studies to screen (not counting duplicates). From these, we judged 14 other studies as relevant. We then inspected all the studies that we deemed relevant (109) in detail and checked whether they still met our

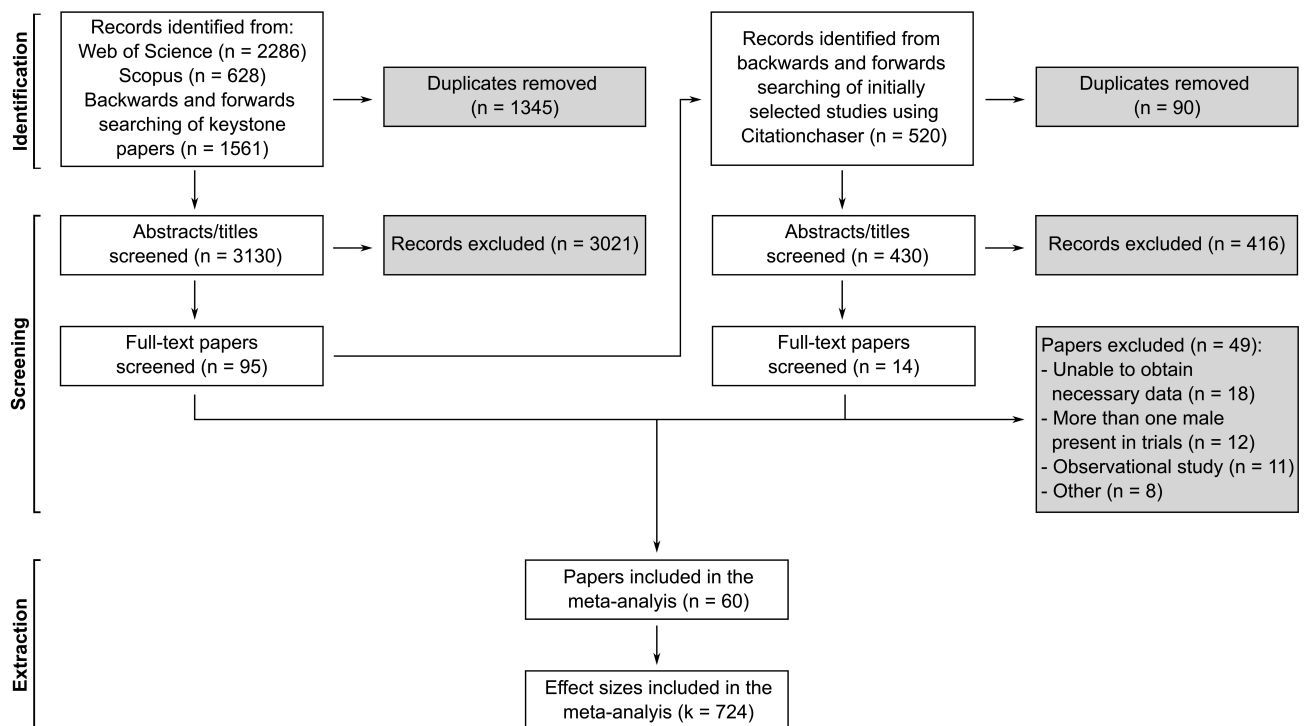


FIGURE 1 PRISMA flow diagram of the data collection process

inclusion criteria. Our combined dataset for our meta-analysis was based on 60 papers, as some of them did not meet our criteria or simply did not show sufficient data to calculate our effect sizes (see Supporting information SI3).

## Inclusion criteria

To be included in our study, the paper had to contain information (explicitly stated in the abstract) regarding the influence of at least one male trait and one female trait on male mating decisions. We considered all male mating decisions as valid: preference proxies and male mating investment from before (e.g. latency to mate, courtship intensity), during (e.g. sperm transferred, copula duration) or after (e.g. guarding duration) copulation. We focused on investigations that used female and male traits that could potentially be connected to our definition of female quality (i.e. related to female benefits to males) and male quality (i.e. related to male-male competition or female mate choice), respectively.

At first, we considered all female traits as valid for inclusion in our meta-analysis, having no filter a priori. However, we later decided to exclude from our meta-analysis selected papers that explored only male mate choice for female receptivity (e.g. arbitrary female behaviours; Bakker & Rowland, 1995; Fernandez et al., 2008) or female social context (Gasparini et al., 2013) because of their unclear connection to our definition of female quality.

Apart from social rank, we only considered intrinsic male characteristics as valid male traits to be included in our meta-analysis (i.e. age, personality, body or body part related traits—linear measurements, area, mass, body condition, colour, morph). Consequently, we did not consider studies that only tested the influence of different environmental conditions (e.g. diet, population density) or male social experiences (e.g. reproductive status) on male mate choice without explicit data on the male traits stated above. We later had to exclude some studies due to our male quality inference methodology (see Data collection and classification section).

We only considered studies that relied on lab or field experiments, as mating patterns from uncontrolled field observations may reflect several mechanisms other than male mate choice (e.g. male-male competition; see Jiang et al., 2013; Moura et al., 2021). Moreover, we only considered studies that used only one male in each trial, otherwise male mating decisions can be influenced by other males (even in female-biased sex ratios; Dougherty, 2020). We made one exception to this rule for Magallón-Gayón et al. (2011), in which a female was given a choice between two males that were tethered and isolated from one another. In that case, once a female chose a male, the couple's interaction could be classified as a no-choice mate choice test from the male perspective. At last, we

only considered studies that tested male mate choice for females of the same species, as mate recognition and mate choice can be distinct processes (Rosenthal, 2017).

## Data collection and classification

We first classified individuals used in experiments according to their phenotypes. Phenotypes could not be included in meta-regressions as continuous variables even when they were available as such because each individual would require its own effect size. Thus, when data related to individual traits were available as continuous variables (from scatter plots, detailed tables, or raw data), we did the following classification that differed between males and females. We classified males in three categories (high, medium, and low trait value; e.g. large, medium-sized, small; old, medium-aged, young; etc) by dividing the range of that male trait in three equal parts. We note that this classification sometimes resulted in low sample size for certain male categories depending on the distribution of sampled individuals, sometimes making it impossible to extract an effect size from a given male category. However, the advantage of using three male categories instead of two is that it better reflects traits that are continuous and allow us to explore whether male mate choice varies gradually or abruptly depending on such traits. We used the original paper's classification when data related to individual traits was not available as continuous data (i.e. categorical data; e.g. dominant and subordinate). We were unable to classify females in three categories because effect size calculation depended on only two means of male mate investment (see Effect size calculation). Thus, we separated females into two categories (high and low trait value; e.g. large and small; old and young; etc) simply by dividing the female trait range (greatest value and lowest value sampled) in two halves.

We inferred individual quality using the individual trait value classification described above coupled with information from the papers we extracted data from (i.e. papers that met our inclusion criteria). We tried to understand how phenotypes from both sexes related to what we considered important to our study: male capacity to acquire mates (male quality) and female reproductive benefits to males (female quality). Such information could be shown by authors through original experiments or by citing species-specific evidence. For example, Hoefler (2007) tested male mate choice with males of different sizes and showed that greater male size in the jumping spider *Phidippus clarus* is associated with greater success in male-male contests. Thus, for that study, we had greater certainty in classifying large males as high-quality, medium-sized males as medium-quality, and small males as low-quality. In other words, we were able to verify the link between the male trait reported in the study and male quality. If male categories were binary

(e.g. dominant and subordinate), we classified them as high and low quality (medium quality inexistent).

Several studies did not provide specific evidence to infer individual quality for the species used in their experiments. When information about female quality was vaguely presented or absent in papers, we inferred female quality based on a general pattern or arbitrarily (see Supporting information S3). In contrast, we did not make any assumptions when the same issue occurred for males. Effect sizes in which male quality could not be verified by the use of phenotypic traits were not used to explore the relationship between the expression of male mate choice and male quality (Table 1). However, if these effect sizes were related to male phenotypes regarding age, body condition, or body size (linear measurements or mass), we still used them to understand whether certain phenotypes are associated with different patterns of male mate choice expression (Table 1, see also Meta-analysis and meta-regressions section). We chose these specific traits because they apply to all species and because they were more often reported in studies than other traits. We thus opted for excluding other male traits of which related quality information was absent (Table 1).

## Effect size calculation

We used standardised mean differences (SMDs) to compare male mating investment between high- and low-quality females. Positive SMDs represent greater male investment to high-quality females than to low-quality females, whereas negative SMDs represent greater male investment to low-quality females than to high-quality females. We note that we also used male mate preference indices as a form of male mating investment. The SMDs we used were analogous to the slope of a preference function, which reflects the strength of mate preference (Edward, 2015). We calculated SMDs for each male quality category, allowing us to test our hypothesis that male mate choice is quality dependent.

**TABLE 1** The hypotheses that we were able to test depending on the male traits examined and whether male quality was verifiable. Hypothesis 1: male mate choice expression depends on male quality. Hypothesis 2: male mate choice expression depends on male phenotype. The 'None' category means that neither hypothesis could be tested. Data in parentheses are the number of papers used to explore the hypothesis

	Male traits	
	Age, body size, body condition	Morph, ornament, personality, social rank
Verifiable male quality	Hypothesis 1 & Hypothesis 2 (N = 29)	Hypothesis 1 (N = 9)
Unverifiable male quality	Hypothesis 2 (N = 29)	None (N = 2)

We calculated SMDs with distinct approaches depending on the nature of the data extracted. First, we used the standard equation for SMD (Borenstein et al., 2021; Cohen, 1988) when male mating investment was given as an absolute measurement for each female (e.g. sperm number):

$$\text{SMD} = \frac{m_{\text{high}} - m_{\text{low}}}{S_{\text{pooled}}} \quad (1)$$

$$S_{\text{pooled}} = \sqrt{\frac{(n_h - 1)sd_h^2 + (n_l - 1)sd_l^2}{n_h + n_l - 2}}, \quad (2)$$

where  $m_h$  and  $m_l$  are the means of male mating investment received by high- and low-quality females, respectively, and  $S_{\text{pooled}}$  is the pooled standard deviation.  $n_h$  and  $n_l$  are sample sizes of high- and low-quality females, respectively, while  $sd_h$  and  $sd_l$  are standard deviations for male mating investment received by high- and low-quality females respectively. We also applied Equation (1) for relative measurements of male mating investment that did not sum one (e.g. figures in Baxter et al., 2015).

Second, when data were already given as a grouped mean difference, we used a slight variation of Equation (1):

$$\text{SMD} = \frac{\bar{m}}{S_{\text{pooled}}}, \quad (3)$$

where  $\bar{m}$  is the mean difference in mating investment that high- and low-quality females received from males. In such cases, the standard deviation given was divided by two and used to calculate  $S_{\text{pooled}}$  as in Equation (2), with  $sd_h = sd_l$ .

Third, when mate choice was shown as binary data (e.g. which female was preferred) or proportions that summed one (e.g. proportion of time spent with each female), we used two other equations to calculate SMDs:

$$\text{SMD} = \frac{\text{logit}(p_h) - \text{logit}(p_l)}{\pi} \sqrt{3}, \quad (4)$$

$$\text{SMD} = \frac{\text{logit}(p_h) - \text{logit}(1 - p_h)}{\pi} \sqrt{3}, \quad (5)$$

where  $p_h$  and  $p_l$  are the mean proportions associated with preference for high- and low-quality females, respectively. We used Equation (4) for no-choice tests, in which a relative measurement of male investment is given for each female (e.g. proportion of trials in which copula occurred for each female type). Equation (5) was used for multiple-choice tests, for which only a single proportion is given (e.g. proportion of trials in which the high-quality female was preferred; mean proportion of association time with the high-quality female). We note

that we assumed the data follows a logistic distribution and thus we used its standard deviation ( $\frac{\pi}{\sqrt{3}}$ ) in place of  $S_{\text{pooled}}$ . When proportions given in studies were extreme (such as when all or none of the males tested preferred large females over small females), we corrected them to a maximum of 0.95 or to a minimum of 0.05 to avoid unrealistic effect sizes.

We calculated the sampling variance for each SMD using the following equations:

$$se_{SMD}^2 = \frac{n_1 + n_2}{n_1 n_2} + \frac{SMD^2}{2(n_1 + n_2 - 2)}. \quad (6)$$

$$se_{SMD}^2 = \frac{2(1 - r_{12})}{n} + \frac{SMD^2}{2(n - 1)}, \quad (7)$$

where  $r_{12}$  is the correlation coefficient between two groups (set as 0.5 in all cases; see Noble et al., 2017) and  $n$  is the trial sample size. We used Equation (6) for effect sizes in which male mating investment given to high-quality females was independent of the male mating investment given to low-quality females. This mainly occurred in studies that used a no-choice design in which males were used a single time. In such cases, we excluded effect sizes whose sum of sample sizes of high- and low-quality females ( $n_h + n_l$ ) was lower than six. In contrast, we used Equation (7) for effect sizes in which male mating investment given to females of different qualities was not independent. This occurred when studies used a multiple-choice design or repeated focal males in no-choice tests. For these cases, we excluded effect sizes whose trial sample size ( $n$ ) was lower than three.

When we calculated SMDs referent to male investment as latency to mate or to court, we inverted the rationale of the equations used: instead of subtracting the investment given to low quality females from the investment given to high quality females, we subtracted the investment given to high quality females from the investment given to low quality females. This is because a preference for high-quality females would generate lower latency (greater responsiveness) with these females than with low-quality females.

We only used descriptive statistics (means and standard deviations) to calculate SMDs. We contacted authors when such information was ambiguous or missing. Within the software R 4.0.3 (R Core Team, 2021), we used the package *metaDigitise* (Pick et al., 2019) to extract data from figures.

## Meta-analysis and meta-regressions

We used multilevel meta-analytical models because our effect sizes were not independent of one another. Different effect sizes could share the same study ID, experiment ID (within each study), investment measurement ID

(within each study), and species ID. Thus, in addition to effect size ID, we used these variables as random factors in our models to control for non-independence. We also included a correlation matrix related to phylogenetic relatedness for the species in our model as a random factor (Nakagawa & Santos, 2012). From meta-analytical models with all these random factors, we quantified total  $I^2$  (a measure of heterogeneity not attributed to sampling error; Higgins et al., 2003) and how much of it each random factor explained (partial  $I^2$ ). Based on this, we removed phylogenetic relatedness from our meta-regressions as this random factor did not explain much of the heterogeneity between effect sizes (partial  $I^2 < 0.001\%$ ) for both of our analyses (see below). In our study, the output from a meta-analytical model with random factors but without any moderators (explanatory variables) represents the average *general* male mate choice (i.e. regardless of male trait values or quality).

We conducted several meta-regressions to test our hypotheses. Using the subset of our data in which male quality was verified (Table 1), we set male quality category (high quality [HQ], medium quality [MQ], or low quality [LQ]) as a moderator to explore whether male mate choice is associated with male quality. To verify whether differences in experimental design and female traits used in empirical studies impact male mate choice expression and the role of male quality in it, we added other moderators as follows. First, we verified the role of female physical contact with males in male mate choice tests (contact allowed vs. contact precluded). Second, we compared the provision of multiple females with a single female to males in male mate choice tests (multiple-choice tests vs. no-choice tests). Third, we evaluated the influence of our method of female quality inference (verified vs. assumed). In addition to conducting meta-regressions with each of these three variables as moderators, we also conducted meta-regressions with these variables in interactions with male quality.

To understand whether male mate choice is dependent on specific male phenotypes, we did an additional meta-regression model including only effect sizes related to certain male traits: age, body condition, and body size (separated in linear measures and mass). In this second model, the moderator was an interaction between these male traits and their values (high trait value, medium trait value, low trait value). We note that we used some of the effect sizes from our first analysis (male quality) in the second one (male phenotypes; Table 1). We note that the results using only the data points for which we had no information on male quality (i.e. exclusive of the second analysis) were very similar to our results with male quality information. However, differences between male quality categories disappeared for linear measures of male size, likely because of lower sample sizes (Supporting information SI5).

All statistical analyses were conducted in the software R 4.0.3 (R Core Team, 2021). We fitted meta-analytical

models using the *rma.mv* function from the package *metafor* (Viechtbauer, 2010). We calculated marginal  $R^2$  (Nakagawa & Schielzeth, 2013), and total and partial  $I^2$  using, respectively, *r2\_ml* and *i2\_ml* functions from the package *orchaRd* (Nakagawa et al., 2021b). Phylogenetic trees were built using the packages *ape* (Paradis & Schliep, 2019) and *rotl* (Michonneau et al., 2016), which uses data from OpenTreeOfLife et al. (2019). We performed pairwise comparisons (z-tests) using the function *glht* from the package *multcomp* (Hothorn et al., 2008). We specifically tested whether the mean effect size of males of higher quality or value trait were different than their counterparts, resulting in three comparisons (high vs. medium, high vs. low, medium vs. low) for each experimental setting (hypothesis 1) and for each male trait (hypothesis 2).

Raw data, analysis script and supplementary materials are available at <https://osf.io/umy4w/>.

## Publication bias

We searched for signs of publication bias in our study using multiple approaches using our full dataset (joined data used for both of our analyses). First, we visually evaluated funnel asymmetry using a funnel plot, which shows the residuals of a meta-analytical model containing all moderators used in our study against effect sizes' precision (i.e. inverse of standard error). Second, we further assessed funnel asymmetry with an alternative approach to Egger's regression: using the inverse of the effective sample size as a moderator in a multilevel meta-analytical model (see Nakagawa et al., 2021a). Third, we verified time-lag bias using publication year as a moderator in a multilevel meta-analytical model.

## RESULTS

### Does male mate choice depend on male quality?

We obtained a total of 336 effect sizes from 38 studies and 32 species for this first analysis (Figure 2a), in which male quality could be verified. On average, males invested moderately more in high-quality females than in low-quality females (Table 2; Figure 3). However, the difference in male mating investment between females of distinct qualities was greater in high- and medium-quality males than in low-quality males (Table 2; Figure 3). Despite these differences, male quality as a moderator explained little of the variance in the data ( $R^2 = 0.015$ ). Heterogeneity across effect sizes was high ( $I^2 = 85\%$ ), with study ID accounting for 3.9% of the heterogeneity, experiment ID accounting for 11.1% of the heterogeneity, measurement ID accounting for 8.8% of the heterogeneity, species ID accounting for 37.1% of the heterogeneity, while the remaining 24.1% of the

heterogeneity was attributed to effect size ID (i.e. residual variance).

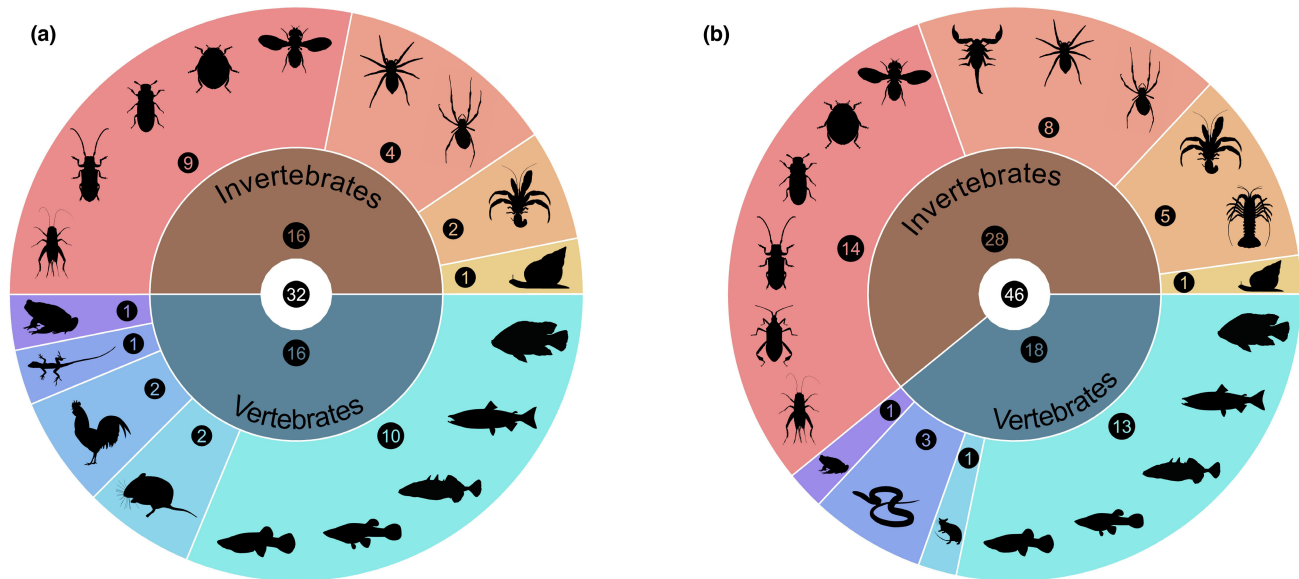
### Does experimental design influence male mate choice patterns related to male quality?

Some aspects from the experimental design of empirical studies we used to extract our effect sizes influenced patterns of interindividual variation in male mate choice. For instance, mean effect sizes differed depending on male quality when males could physically interact with females during experiments, but not when males were precluded from interacting with females (Table 2, Figure 4). Similarly, mean effect sizes differed depending on male quality when males were presented with more than one female in experiments, but not when males were presented with a single female (Table 2, Figure 4). Moreover, mean effect sizes differed depending on male quality regardless of whether female quality was verified (Table 2, Figure 4). Nonetheless, when female quality was assumed, the only difference in mean effect sizes between male quality categories was between medium- and low-quality males. A meta-analytical model with these three aspects as moderators interacting with male quality increased some of the variance explained ( $R^2 = 0.073$ ).

### Does male mate choice depend on male phenotype?

We obtained a total of 674 effect sizes from 53 studies and 46 species for our analysis related to male mate choice expression for certain male phenotypes (specifically regarding male age, body condition, body size; Figure 2b). Similar to our results regarding male quality, on average, males of all phenotypes invested moderately more in high-quality females than in low-quality females (SMD = 0.524, CI = 0.351 to 0.696). Heterogeneity across effect sizes was high ( $I^2 = 78.5\%$ ), with study ID accounting for 33.9% of the heterogeneity, experiment ID accounting for 13.9% of the heterogeneity, measurement ID accounting for 1.3% of the heterogeneity, species ID accounting for 9.5% of the heterogeneity, while the remaining 19.9% of the heterogeneity was attributed to effect size ID (i.e. residual variance).

The difference in male mating investment between females of distinct qualities was greater in males with great body condition than in males with low body condition (Table 3, Figure 5). In comparison, males with medium body condition showed an intermediate mean effect size value, which was not statistically different from males in great or low body condition (Table 3, Figure 5). The relationship between the strength of male mate preference and male size depended on how it was measured. Considering only linear measures of body size (e.g. length, width), the difference in male mating investment



**FIGURE 2** Number of species of each animal taxa in our datasets regarding the role of male quality (a) and male phenotype (b) on male mate choice expression. Silhouettes illustrate certain species used from each group. From the yellow section, in anti-clockwise order: molluscs, crustaceans, arachnids, insects, amphibians, non-avian reptiles, birds (only in the first dataset), mammals and fish

between females of distinct qualities was greater in large and medium-sized males than in small males (Table 3, Figure 5). In contrast, there was no difference of mean effect sizes between males of different body mass (Table 3, Figure 5). Similarly, there was no difference of mean effect sizes between males of different age (Table 3, Figure 5). Using male trait, male trait value, and their interaction as moderators explained little of the variance in the data ( $R^2 = 0.029$ ).

### Was publication bias detected?

Our funnel plot suggests funnel asymmetry as there are more extreme positive residuals than negative ones (Figure 6). However, a meta-analytical regression using the square-root of the inverse of the effective sample size as a moderator shows that effect size values are not predicted by effective sample size (coefficient estimate =  $-0.05$ ; CI =  $-0.11$  to  $0.01$ ; Figure 7a). In contrast, more recent publications contained lower effect size values, indicating time-lag publication bias (coefficient estimate =  $-0.25$ ; CI =  $-0.38$  to  $-0.13$ ; Figure 7b).

## DISCUSSION

In this study, we carried out the first synthesis and meta-analytical exploration regarding interindividual variation of male mate choice. We did not find support for our prediction that male mate choice is assortative regarding male quality, or that low-quality males are indiscriminate in their mate choice, as males of all quality categories prefer high-quality females (varying from

moderate to high magnitude, Cohen, 1988). However, we found that high- and medium-quality males are, on average, choosier than low-quality males, meaning that male quality is associated with different strengths of mate preference. We also did not find support for our prediction that males with different size, body mass, age, and body condition had different mate preferences. Nonetheless, we found that the strength of male mate preference varies with male body size and body condition (but not with male body mass and age). This means that assuming male quality solely on male phenotype may lead to different patterns of male mate choice expression. We also found that certain methodological aspects from empirical studies can have an impact on our general findings, i.e. differences in experimental design can have a strong effect on our understanding of male mate choice. As such, readers should also take our results with an understanding of the limitations of the data provided.

### Does male mate choice depend on male quality?

Theoretical studies indicate that males may express mate choice differently according to their quality (Chevalier et al., 2020; Fawcett & Johnstone, 2003; Härdling et al., 2008; Härdling & Kokko, 2005; Puurtinen & Fromhage, 2017; Venner et al., 2010). Yet, there is not a consensus among these studies on the exact pattern that should arise for male mate choice expression related to male quality. This is because theoretical studies model a plethora of ecological variables that can modulate how male quality influences fitness outputs from male decisions, including male mate choice. Although often restricted to certain



**TABLE 2** Male mate choice effect sizes and pairwise comparisons for each male quality category and experimental design

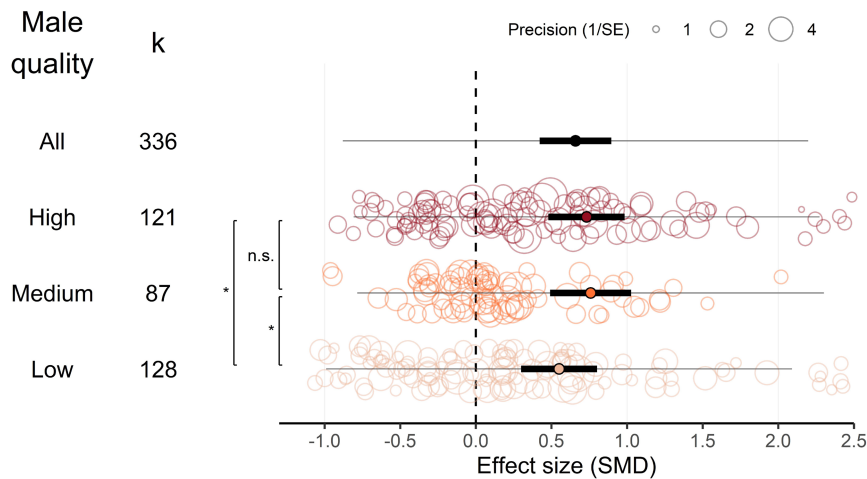
Experimental design subsets	Male quality category	k	Effect size mean	CI lower bound	CI upper bound	Pairwise comparisons*	
						vs. medium-quality male	vs. low-quality male
- †	All	336	0.659	0.422	0.896	–	–
	High	121	0.732	0.48	0.985	0.323 (0.747)	<b>2.363 (0.018)</b>
	Medium	87	0.759	0.491	1.027	–	<b>2.415 (0.016)</b>
	Low	128	0.55	0.299	0.802	–	–
Contact allowed‡	All	224	0.781	0.506	1.057	–	–
	High	83	0.869	0.574	1.164	0.083 (0.934)	<b>2.068 (0.039)</b>
	Medium	51	0.86	0.535	1.185	–	1.62 (0.105)
	Low	90	0.672	0.376	0.967	–	–
Contact precluded‡	All	112	0.444	0.094	0.793	–	–
	High	38	0.482	0.098	0.868	0.651 (0.515)	1.096 (0.273)
	Medium	36	0.567	0.179	0.955	–	1.737 (0.082)
	Low	38	0.337	–0.042	0.716	–	–
Multiple-choice‡	All	170	0.713	0.43	0.996	–	–
	High	60	0.827	0.522	1.131	0.783 (0.434)	<b>2.976 (0.002)</b>
	Medium	48	0.913	0.591	1.234	–	<b>3.584 (&lt;0.001)</b>
	Low	62	0.52	0.22	0.82	–	–
No-choice‡	All	166	0.555	0.169	0.942	–	–
	High	61	0.574	0.172	0.976	0.653 (0.514)	0.155 (0.877)
	Medium	39	0.494	0.061	0.927	–	0.467 (0.64)
	Low	66	0.557	0.153	0.96	–	–
Verified female quality‡	All	178	0.673	0.423	0.922	–	–
	High	59	0.808	0.531	1.085	0.8 (0.424)	<b>2.384 (0.017)</b>
	Medium	52	0.72	0.432	1.007	–	1.469 (0.142)
	Low	67	0.556	0.279	0.833	–	–
Assumed female quality‡	All	158	0.642	0.381	0.902	–	–
	High	62	0.647	0.362	0.932	1.343 (0.179)	1.029 (0.303)
	Medium	35	0.815	0.505	1.125	–	<b>2.113 (0.035)</b>
	Low	61	0.533	0.236	0.83	–	–

\*z-scores are given along with *p*-values (in parentheses), bold font indicates significant differences ( $p < 0.05$ ). †No (overall average) or only male category as moderator. ‡Experimental design and its interaction with male quality category as moderators. k is the number of effect sizes in each category and CI refers to the effect sizes' 95% confidence interval.

scenarios, a pattern that arises in all the theoretical studies cited above is that male mate choice expression can be assortative in respect to quality. Alternatively, another pattern predicted is that low-quality males are simply non-choosy regarding their mates. We used these patterns to predict our results, but we did not find support for them: all males, on average, prefer high- over low-quality females (i.e. they invest more resources in the former than in the latter). However, on average, high and medium-quality males show greater strength of mate preference than low-quality males. Our findings may suggest that the net benefit for males of being choosy depends only weakly on male quality or, alternatively, that such dependence varies across species (resulting in lower average differences). We note that our study aimed to examine average differences between males of distinct

qualities in male mate choice expression, but that patterns of male mate choice expression in nature vary and that such variation is predicted by theoretical studies. While male quality indeed affects male mate choice only in strength in some species (e.g. Ng & Williams, 2014; Sato et al., 2006; Sato & Goshima, 2007b), it can influence the direction of male mate preference in others (e.g. Baldauf et al., 2013; Pollo et al., 2019). Thus, our results showing that male quality plays a role in male mate choice expression in a nuanced pattern should not be interpreted as a norm for all animals, but rather highlight the importance of considering male quality in male mate choice assays.

In our meta-analysis, we only included empiric studies in which males were in a non-competitive scenario. Thus, one assumption of our study is that males are able



**FIGURE 3** Mean effect sizes for male mate choice according to each male quality category. Positive values represent that males invest more in high-quality females than in low-quality females. Thick horizontal lines represent 95% confidence interval and thin horizontal lines represent prediction interval.  $k$  is the number of effect sizes in each category. A star represents significant differences between means of distinct male quality categories (z-tests with  $p < 0.05$ ), while n.s. represents non-significant differences. There are data points not shown with values lower or greater than the limits of the x-axis in this figure

to assess their own quality and then express mate choice that is optimal based on their assessment. It is possible that, at least in some species, males of different qualities primarily prefer high-quality females, but become unselective after being rejected or losing contests. This would be a carry-over effect similar to the ‘loser effect’, in which males decrease their fighting ability after losing a previous contest (e.g. Kasumovic et al., 2010). In other words, experience may modulate future male mate preference. Alternatively, male quality may only influence male mate choice expression in certain contexts, such as when competition intensity is high (e.g. Bel-Venner et al., 2008) or when males are in the presence of competitors (e.g. Jordan et al., 2014). Although a recent meta-analysis explored whether mate choice depends on context (Dougherty, 2021), it did not explore contexts related to competition. Thus, synthesising how experience and competition-related contexts influence mate choice should be a fruitful next step.

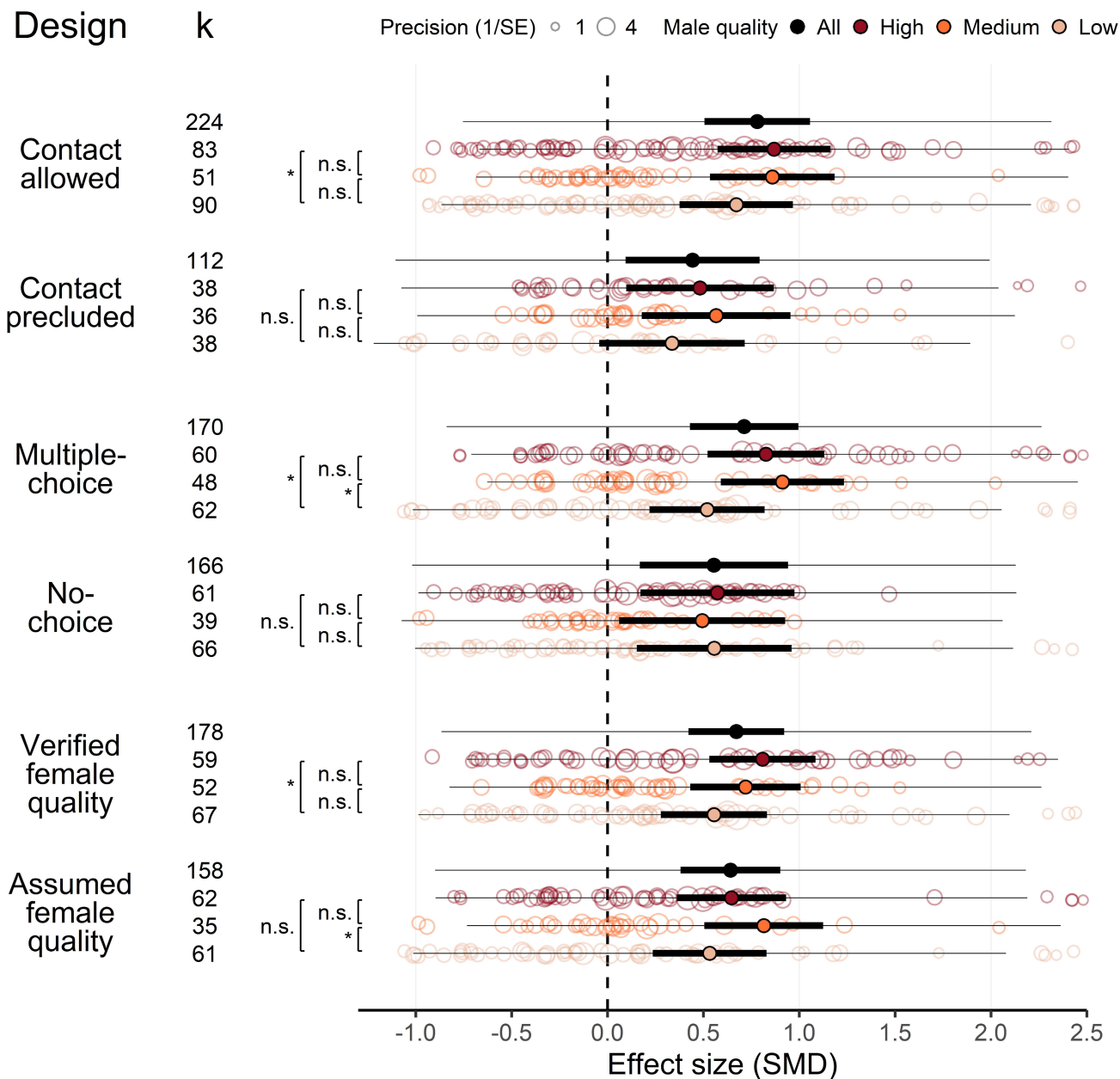
### Does experimental design influence male mate choice patterns related to male quality?

The experimental design of the studies we extracted our effect sizes from influenced patterns of male mate choice expression. The difference in male investment between high- and low-quality females was, on average, greater for high-quality males than for low-quality males only when males were allowed to physically interact with females and when multiple females were presented to males in experiments. It is possible that females influenced the amount of resources they received from males when individuals could physically interact in experiments, which suggests that interpreting our effect sizes exclusively as male mate choice may be erroneous to some degree. Alternatively,

the differences we found related to physical contact may have occurred because there were fewer studies in which males were precluded from physically interacting with females, generating wider confidence intervals and consequently decreasing the chance that small differences across male quality categories could be detected.

We also found that patterns of male mate choice expression vary with the number of females presented to males in experiments. Dougherty and Shuker (2015) found (also using a meta-analytical approach) that individuals tend to be choosier when multiple prospective mates are available, given that in such scenarios being choosy should be less costly. Our results do not support this as we found that, across effect sizes, the strength of male mate preference is only slightly lower in no-choice than multiple-choice experiments ( $z = -0.675$ ,  $p = 0.5$ ). Yet, we found that this decrease occurred more strongly in high- and medium-quality males than in low-quality males, so that male mate choice expression in no-choice experiments does not vary across male quality categories. The differences we found in male mate choice expression due to distinct experimental design may be an indicator that the role of male quality on male mate choice is context-specific.

Our method of female quality inference also impacted the pattern we observed in male mate choice expression, as we found a difference in choosiness between high- and low-quality males when female quality was verified, but not when it was assumed. Male mate choice is often associated with males seeking direct benefits from females, such as greater fecundity and lower sperm competition risk. Indeed, female traits in our dataset represent these direct benefits when female quality could be verified. However, our results show that assumptions on female quality may be problematic for male mate choice studies and hence should be avoided.



**FIGURE 4** Mean effect sizes for male mate choice according to male quality under different experimental designs. Positive values represent that males invest more in high-quality females than in low-quality females. Thick horizontal lines represent 95% confidence interval and thin horizontal lines represent prediction interval. k is the number of effect sizes in each category. A star represents significant differences between means of distinct male quality categories (z-tests with  $p < 0.05$ ), while n.s. represents non-significant differences. There are data points not shown with values lower or greater than the limits of the x-axis in this figure

### Does male mate choice depend on male phenotype?

Our study also explored whether assuming male quality from generalisations based on certain male traits influences male mate choice expression. More specifically, we verified whether male mate choice varies with male age, body size, and body condition, without necessarily knowing whether or how such traits affect male quality in a given species. We found that males that are large and in great body condition are choosier than males that are small and in low body condition, but that old and

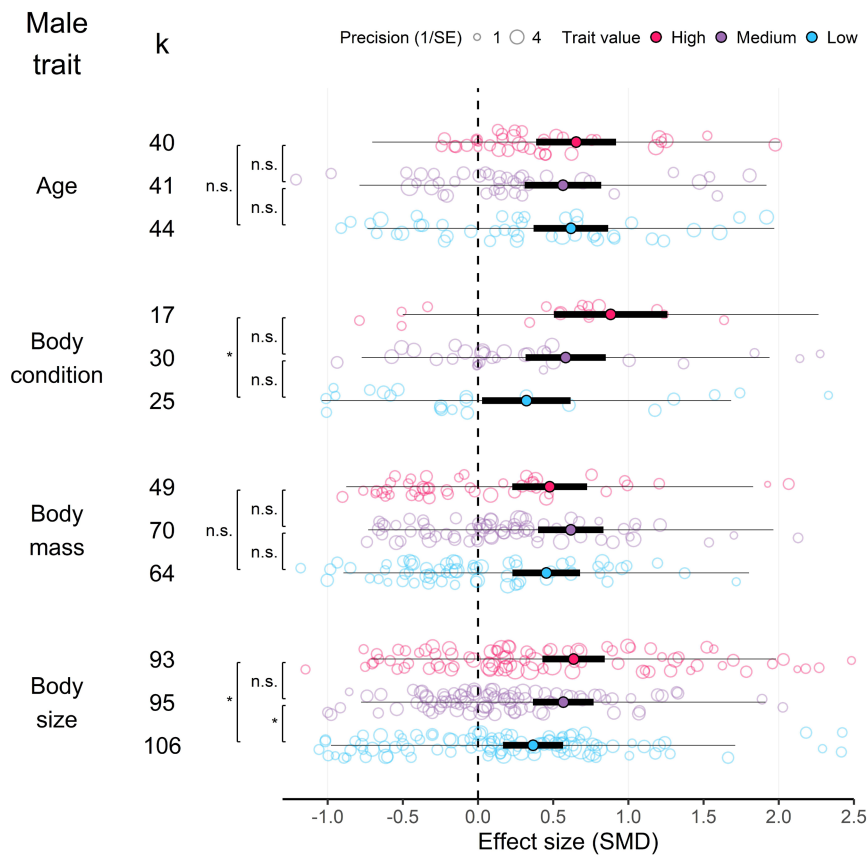
heavy males express similar preference strength to young and light males. These results are likely a product of differences regarding the relationship between these male traits and male quality, i.e. whether male age, body size, and body condition really predict male quality consistently in several species. Here, we briefly speculate about this relationship, but we emphasise that this matter deserves its own investigation.

The relationship between male age and male quality appears to be conflicting. Older males should be more attractive if greater age reflects good genes (Kokko, 1998). On the other hand, females may avoid older

**TABLE 3** Male mate choice effect sizes and pairwise comparisons for each male trait value category and male trait

Male trait	Male trait value category	k	Effect size mean	CI lower bound	CI upper bound	Pairwise comparisons*	
						vs. medium trait value	vs. low trait value
Age	High (old)	30	0.653	0.388	0.918	0.717 (0.474)	0.304 (0.761)
	Medium	24	0.565	0.311	0.82	–	0.465 (0.642)
	Low (young)	28	0.618	0.37	0.866	–	–
Body condition	High	12	0.883	0.506	1.26	1.551 (0.121)	<b>2.84 (0.005)</b>
	Medium	26	0.583	0.316	0.85	–	1.753 (0.08)
	Low	20	0.322	0.028	0.617	–	–
Body mass	High (heavy)	23	0.477	0.228	0.726	1.331 (0.183)	0.205 (0.838)
	Medium	41	0.617	0.4	0.835	–	1.777 (0.076)
	Low (light)	35	0.454	0.23	0.679	–	–
Body size	High (large)	45	0.636	0.429	0.843	0.854 (0.393)	<b>3.377 (&lt;0.001)</b>
	Medium	50	0.568	0.366	0.77	–	<b>2.607 (0.009)</b>
	Low (small)	54	0.367	0.167	0.566	–	–

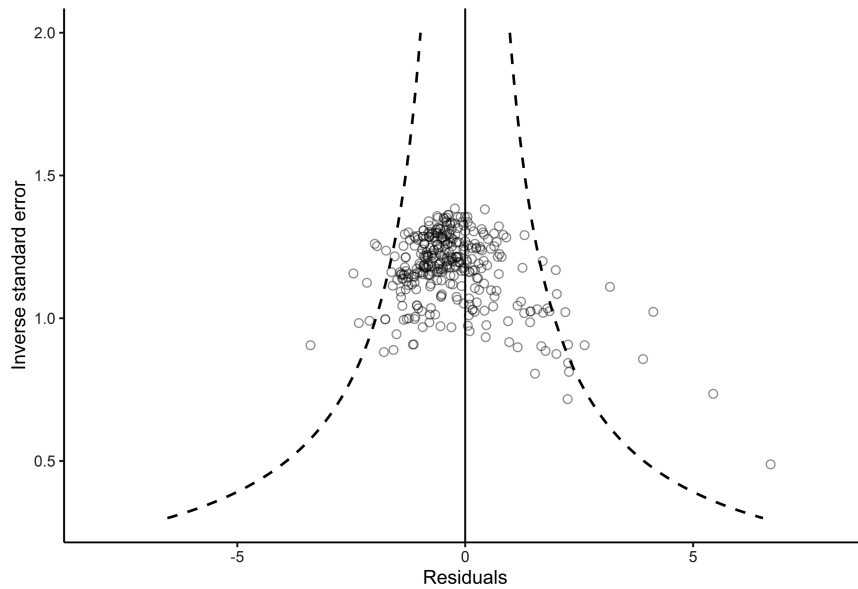
\*z-scores are given along with *p*-values (in parentheses), bold font indicates significant differences ( $p < 0.05$ ). *k* is the number of effect sizes in each category and CI refers to the effect sizes' 95% confidence interval.



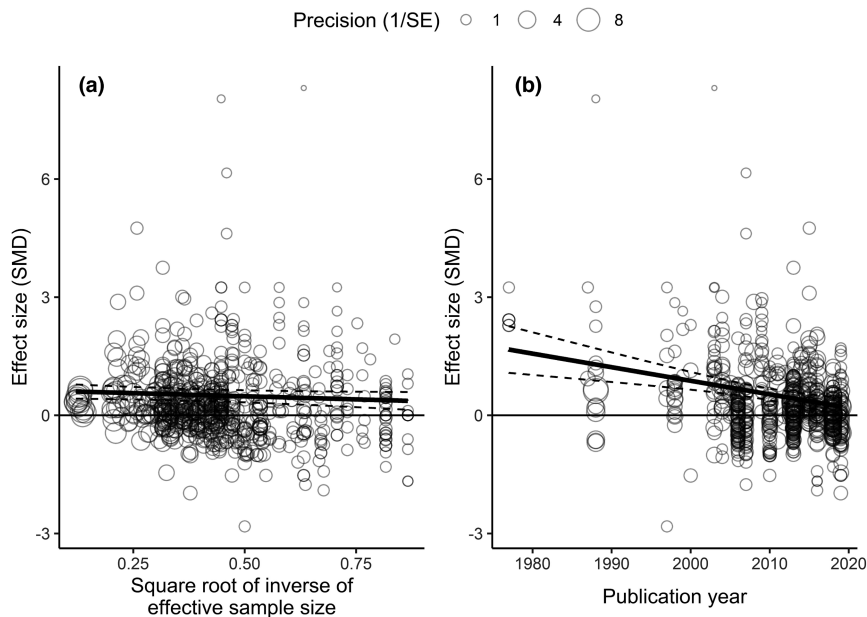
**FIGURE 5** Mean effect sizes for male mate choice according to male phenotypes, for different male traits. Positive values represent that males invest more in high-quality females than in low-quality females. Thick horizontal lines represent 95% confidence interval and thin horizontal lines represent prediction interval. *k* is the number of effect sizes of each phenotype. A star represents significant differences between means of distinct male trait value categories (z-tests with  $p < 0.05$ ), while n.s. represents non-significant differences. There are data points not shown with values lower or greater than the limits of the x-axis in this figure

males if they reduce female fitness (e.g. Bista & Omkar, 2015), given that they often produce ejaculates of lower quality (e.g. Johnson et al., 2018; Vega-Trejo et al.,

2019). Thus, it is likely that the relationship between male age and quality is inconsistent enough so that no clear pattern between male age and male mate choice



**FIGURE 6** Funnel plot of the residuals of a meta-analytical model using data on male mate choice expression with several moderators (see Material and methods)



**FIGURE 7** Assessments of publication bias. (a) Relationship between effect size (SMD) and square root of inverse of effective sample size. (b) Relationship between effect size (SMD) and publication year. Broken lines represent 95% confidence intervals for regression estimates

expression arises. In addition, mate choice should be more costly for older males because they are more likely to die. As a consequence, older males should be less choosy as any mating opportunity could be their last. Regardless of the reason, our results suggest that male age does not consistently influence male mate choice expression as other male traits, such as body size and body condition, do.

The influence of male body size and male body condition on male quality has been well documented (Andersson, 1994). Even when these traits are not directly sexually selected, they may predict male quality

due to their relationship to the expression of male weapons and ornaments (Andersson, 1994; Johnstone, 1995; Emlen, 2008; e.g. Contreras-Garduño et al., 2008). Thus, it is expected that the effect of these traits on male mate choice expression would be similar to the effect of verified male quality. Yet, it is difficult to understand why male linear measures of size influence male mate choice, but male body mass does not. It could be that body mass is not as consistently related to male quality because it is more labile than structural body size, as the latter is constant once individuals reach maturity in several taxa. If body mass tends

to change quickly, there would be weaker selection for males to use their body mass as a behavioural compass. However, this rationale would also affect body condition, which is usually calculated by taking the residuals of a linear regression of body mass on a linear measure of body size (Jakob et al., 1996). This questions why we see the pattern we do in body condition, but not body mass. It is possible that our results for body condition are misrepresented, as our data for this trait (with the exception of one study) was a subset of the studies that also report body mass. This would be plausible if researchers tend to report body condition indices only when body mass influences male mate choice expression.

## Implications

Evolutionary biologists often argue in favour of the sex-stereotypification of behavioural expression, often summoned in the motto 'males fight, females choose' (criticised by Pollo & Kasumovic, 2022; Tang-Martinez, 2016). Our study counters this rationale with evidence that males of all qualities, on average, prefer high-quality females over low-quality females. This, however, may be contested because our methodology was not intended to synthesise the mate preference strength for all males, as we only used studies that explored interindividual variation in male mate choice. Still, we highlight that the strength of male mate preference increases with male quality and that it could be a crucial factor when assessing mate choice. By treating all males homogeneously, one can overview the existence of male mate choice.

## Caveats and recommendations

Our results depend on the assumption that our datasets are unbiased and representative samples of the role of male quality and male phenotype on male mate choice in nature. We did not find strong evidence of publication bias as effect sizes with smaller precision do not have greater values. Yet, as in many meta-analyses, older studies tended to report greater effect sizes than more recent ones. This may have happened because journals were less prone to accept small effect sizes or 'non-significant' results in the past (Koricheva et al., 2013). We also note that our datasets showed high heterogeneity (although most of it was controlled in our multilevel models) and that our moderators did not explain much of the variance in the data, suggesting that there may be other factors relevant to the expression of male mate choice than the ones explored in our study.

As other meta-analyses, our study critically depends on certain logistic decisions. In particular, classifying males and females according to their quality was central for our study. Existing definitions of the term 'quality' can be difficult to use empirically as they focus on the

relationship between an individual's phenotype and its fitness (Wilson & Nussey, 2010). We solely focused on the relationship between female phenotypes and their reproductive benefits to males, and on the relationship between male phenotypes and male capacity to acquire mates (i.e. attractive or fighting ability). Even though there may be some overlap in our use of the term and Wilson & Nussey's definition, we were interested in how phenotypes influenced proximate processes, not in their ultimate consequences to fitness. For example, female size in fruit flies positively correlates with fecundity (Sisodia & Singh, 2004), reflecting female quality according to our definition (benefits to males) and Wilson & Nussey's definition of quality (female fitness). In contrast, female age is a transient trait and hence has no relation to female fitness, but can impact fecundity (e.g. Dhole & Pfennig, 2014) and consequently the female reproductive benefits to males. In addition, our approach has limitations as we could not control the magnitude of differences between high- and low-quality of both males and females across species and traits. For instance, high-quality males could be five times more attractive to females (e.g. likely to be chosen) than low-quality males in a given species, but only two times in another one. Yet, this is a unescapable situation in meta-analyses in the field of ecology and evolution, especially when working with a broad phylogenetic scope as we do here.

Two factors in our study can decrease the generality of our results. First, as previously mentioned, our results were sensitive to the experimental design used in empirical papers. We thus advise empiricists to employ multiple settings in their experiments (see Dougherty, 2020) to understand how experiment design mediates the expression of male mate choice with more precision. If not possible, empiricists should prioritise methods in which males cannot physically interact with females to ensure that any male decisions are free of female influence. Second, most of our data comes from two taxonomic groups: fish and insects. To ameliorate such taxonomic bias, we recommend that empiricists evaluate mate choice in mammals, birds, reptiles, amphibians and non-arthropod invertebrates, even when there is no apparent reason to believe that males are choosy.

## Conclusion

In this study, we show that male quality plays a role in male mate choice expression: greater male quality increases choosiness. Furthermore, we show that body size and body condition are key male traits given they are connected to differences in male mate choice expression while other traits are not. We also emphasise that male mate choice is a complex behavioural process that can be influenced by several other factors (as seen

by high heterogeneity and differences across distinct experimental designs), and that these factors can also modulate the dependency of male mate choice on male quality. Thus, we strongly recommend more research on male mate choice expression to uncover its complexity, as our knowledge about it is minimal, especially when compared with female mate choice.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHORSHIP

Pietro Pollo: Conceptualisation, Methodology, Formal Analysis, Investigation, Data Curation, Writing – Original draft, Writing – Review & Editing, Visualisation, Project administration. Shinichi Nakagawa: Methodology, Writing – Review & Editing, Supervision, Project Administration. Michael Kasumovic: Conceptualisation, Writing – Review & Editing, Supervision, Project Administration.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13981>.

## OPEN RESEARCH BADGES



This article has earned Open Data Design badge. Data design and analysis plan are available at: [10.17605/OSF.IO/UMY4W](https://doi.org/10.17605/OSF.IO/UMY4W).

## DATA AVAILABILITY STATEMENT

Data, analysis scripts and supporting information are available at <https://osf.io/umy4w/>.

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