Synthesis of sexual selection: a systematic map of meta-analyses with bibliometric analysis

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ABSTRACT

Sexual selection has been a popular subject within evolutionary biology because of its central role in explaining odd and counterintuitive traits observed in nature. Consequently, the literature associated with this field of study became vast. Meta-analytical studies attempting to draw inferences from this literature have now accumulated, varying in scope and quality, thus calling for a synthesis of these syntheses. Here, we conducted a systematic literature search to create a systematic map with a report appraisal of meta-analyses on topics associated with sexual selection, aiming to identify the conceptual and methodological gaps in this secondary literature. We also conducted bibliometric analyses to explore whether these gaps are associated with the gender and origin of the authors of these meta-analyses. We included 152 meta-analytical studies in our systematic map. We found that most meta-analyses focused on males and on certain animal groups (e.g. birds), indicating severe sex and taxonomic biases. The topics in these studies greatly varied, from proximate (e.g. relationship of ornaments with other traits) to ultimate questions (e.g. formal estimates of sexual selection strength), albeit the former were more common. We also observed several common methodological issues in these studies, such as lack of detailed information regarding searches, screening, and analyses, which ultimately impairs the reliability of many of these meta-analyses. In addition, most of the meta-analyses' authors were men affiliated to institutions from developed countries, pointing to both gender and geographical authorship biases. Most importantly, we found that certain authorship aspects were associated with conceptual and methodological issues in meta-analytical studies. Many of our findings might simply reflect patterns in the current state of the primary literature and academia, suggesting that our study can serve as an indicator of the issues within the field of sexual selection at large. Based on our findings, we provide both conceptual and analytical recommendations to improve future studies in the field of sexual selection.

Keywords: sexual signals, weapons, mate choice, intrasexual competition, sperm competition, polyandry, extra-pair fertilisations, mating success, taxonomic chauvinism, gender bias.

CONTENTS

I. INTRODUCTION

(1) Background

Colourful and exaggerated body parts have intrigued many long before the foundation of evolutionary biology. The concept of sexual selection emerged to explain the existence of these odd traits, whose evolution by natural selection seemed improbable as some of them appeared only to hinder the survival of their bearers (Hosken & House, 2011; Ruse, 2015). Darwin (1859, 1871) initially postulated sexual selection as the struggle of males for access to females, but later referred to it as the reproductive advantage that some individuals have over same sex conspecifics. Since then, the definition of sexual selection has been repeatedly debated and reformulated, mostly to include relevant post-copulatory processes and to clarify in which scenarios sexual selection indeed occurs (reviewed in Gowaty, 2015; Alonzo & Servedio, 2019; e.g. Andersson, 1994; Clutton-Brock, 2007; Shuker & Kvarnemo, 2021a). Despite the everlasting discussions on what sexual selection encapsulates, a vast field of study has grown within evolutionary biology centred on topics intimately around this concept. From extravagant traits and mechanisms selecting them to formal estimates of sexual selection, the literature related to sexual selection became diverse and deeply interconnected. Summarising our understanding of the entire field thus represents a challenging endeavour, albeit theoretically a possible one.

To be able to generalise results and advance science, one can combine knowledge from different individual investigations (Jennions *et al.*, 2012). Systematic reviews and meta-analysis are considered the gold standard for such comprehensive evidence synthesis (Koricheva, Gurevitch & Mengersen, 2013; Borenstein *et al.*, 2021). This is because systematic reviews aim to detect all the studies conducted on a certain topic, while meta-analyses additionally provide quantitative measures related to the average and dispersion of studies' outcomes by standardising (effect sizes) and weighting them by their precision coupled with solid statistical techniques (Jennions *et al.*, 2012; Gurevitch *et al.*, 2018; Borenstein *et al.*, 2021). It is unsurprising then that many meta-analyses have been conducted to test long standing hypotheses of topics relevant to sexual selection. Jennions *et al.* (2012) reviewed 94 of these meta-analyses, summarised their content, and identified opportunities for future synthesis studies. Yet, several other meta-analyses in this field have accumulated during the more than a decade since Jennions *et al.* (2012), suggesting that a new audit of the knowledge provided by these studies is warranted. This can be achieved with a systematic map (sometimes called an evidence map): a systematic synthesis of a broad topic in a digestible format (e.g. with visual depictions of the data) that aims to identify knowledge gaps rather than to describe research findings (Miake-Lye *et al.*, 2016; O'Leary *et al.*, 2017; Sutherland & Worldley, 2018).

Meta-analyses should follow reporting guidelines to ensure transparency and reproducibility (e.g. PRISMA: Page *et al.*, 2021; O'Dea *et al.*, 2021; AMSTAR 2: Shea *et al.* 2017; MOOSE: Stroup *et al.*, 2000). However, they often neglect some or all of these directives, especially older meta-analyses (when such guidelines had not been established yet). Therefore, it is crucial to not only understand the content of meta-analyses related to sexual selection relevant topics, but to assess their reporting quality to ensure reproducibility. This type of appraisal was not present in Jennions *et al.* (2012), leaving an important gap in our comprehension of the field related to sexual selection. Such appraisal will also be useful to determine which meta-analyses might require re-evaluation and updating. Moreover, we can use information on reporting quality in published sexual selection meta-analyses to provide an evidence-based set of recommendations to improve future meta-analytical studies in this and other fields.

Bibliometrics represents another set of tools that can improve our understanding of a field and its patterns. That is because bibliometrics provide quantitative information on authors and collaborative networks. Such information could be used to improve gender and geographical representation of research topics, addressing issues around equity, diversity, and inclusiveness (Davies *et al.*, 2021). Traditionally, systematic reviews (and maps) concentrated on the existing research content, avoiding discussions on who conducted it (Nakagawa *et al.*, 2019). Yet, given the historic conceptual 'male-centeredness' in the topic of sexual selection (Ah-King, 2022a, 2022b), it may be of particular importance to examine the diversity and inclusiveness of authors of meta-analyses related to sexual selection. To our knowledge, this has never been done for sexual selection research, uncovering an exciting opportunity for this field.

(2) Objectives

Our main aim was to provide insights and identify gaps in the sexual selection literature by conducting a systematic map of existing meta-analyses on topics related to this field. We used a novel method called "research weaving", which combines a systematic map with bibliometric analysis (Nakagawa *et al.*, 2019). In addition, we conducted a report appraisal of the included meta-analyses. We aimed to answer the following questions related to sexual selection and associated topics, based on the collated dataset:

1. What is the scope of existing meta-analyses?
    1. Where are the gaps in the evidence syntheses, requiring more attention or updates? See section III.2.
    2. What are the conceptual challenges in this field and how to address them? See section III.3.

2. What methodological patterns are observed in existing meta-analyses?
    1. How transparent and robust are existing meta-analyses? See section III.4.
    2. What are the methodological challenges in this field and how to address them? See section III.5.
3. Who and from where are researchers that conducted existing meta-analyses?
    1. Is authorship diversity associated with conceptual and methodological patterns in existing meta-analyses? See section III.6.

II. METHODS

Our methodology was described in our pre-registration (Pollo *et al.*, 2023), and we adhered to it as much as possible. However, we adjusted several elements to improve the manuscript. These adjustments are mentioned throughout the manuscript when applicable (see also Supplementary material for a summary of these adjustments). We broadly followed the guidelines of ROSES for reporting of systematic maps (Table S1; Haddaway *et al.*, 2018). We report author contributions using MeRIT guidelines (Nakagawa *et al.*, 2023) throughout the manuscript and the CRediT statement (McNutt *et al.*, 2018) at the end of it.

(1) Literature searches

PP conducted literature searches using six different sources, all on March 15th, 2023. First, we conducted a main database search using Scopus and Web of Science (Core Collection), both accessed through the University of New South Wales, Sydney. For this, we created strings with keywords aimed to capture meta-analytical studies on non-human animals that cover one or more topics relevant to sexual selection (see Supplementary material and section II.2). Second, we retrieved the backward and forward citations from Jennions *et al.* (2012)

(i.e. list of citations and studies that cited it, respectively). Third, to find relevant grey literature, we used a simplified keyword string (“meta-analysis” AND “sexual selection”) in Bielefeld Academic Search Engine (BASE), filtering only theses (doctype:18*). Fourth, we conducted several searches in Google Scholar using translations of the string used in BASE in languages that at least one person from our team could understand: Simplified and Traditional Chinese, Croatian, Japanese, Polish, Portuguese, Russian, and Spanish (see Supplementary material for details). However, we only screened the ten first results from each of these Google Scholar searches, sorted by relevance. We planned to screen 10 more if at least half of the previous 10 contained relevant articles, but that was not the case for any language. Additionally, we manually included four studies that were not captured by our searches (Janicke *et al.*, 2018; Aguiar Del Matto, 2018; Gómez-Llano *et al.*, 2023; Dougherty, 2023). A pilot conducted for our pre-registration (see Pollo *et al.* 2023) found that these searches retrieved relevant benchmark articles, ensuring that our searches were comprehensive.

(2) Screening process and inclusion criteria

Our screening criteria are summarised in Table 1 (but see the details in the Supplementary material) and our screening process is shown in Figure 1 (slightly different from the one in our pre-registration but conceptually identical; see Pollo *et al.* 2023). We used Rayyan QCRI (Ouzzani *et al.*, 2016) for both the initial and the full-text screenings. ML and PP independently conducted the initial screening, i.e. assessed the title, abstract, and key-words of retrieved studies. The full-text content of studies that passed the initial screening were then independently assessed by two people: PP (100%) and either AC, ML, SN, or YY (in roughly

29%, 14%, 28%, and 29% of the cases, respectively). In both initial and full-text screening, authors solved conflicts through discussion until consensus was reached.

Table 1. Scope of our systematic map of meta-analyses on topics related to sexual selection, according to the PECOS framework.

Population	Non-human animals (occasionally other organisms as well if they are included in meta-analyses with non-human animals, but we do not use details of these other organisms in our manuscript).
Exposure	Factors that potentially affect mechanisms and patterns related to sexual selection.
Comparator	Not applicable.
Outcomes	Outcomes related to patterns and consequences on core topics of sexual selection, such as sexual traits and signals, mate choice, intrasexual competition, pairing and mating decisions, sexual selection estimates, and interlocus sexual conflict.
Study-design	Meta-analyses (*sensu* O'Dea *et al.* 2021: statistical synthesis of effect sizes from multiple independent studies).

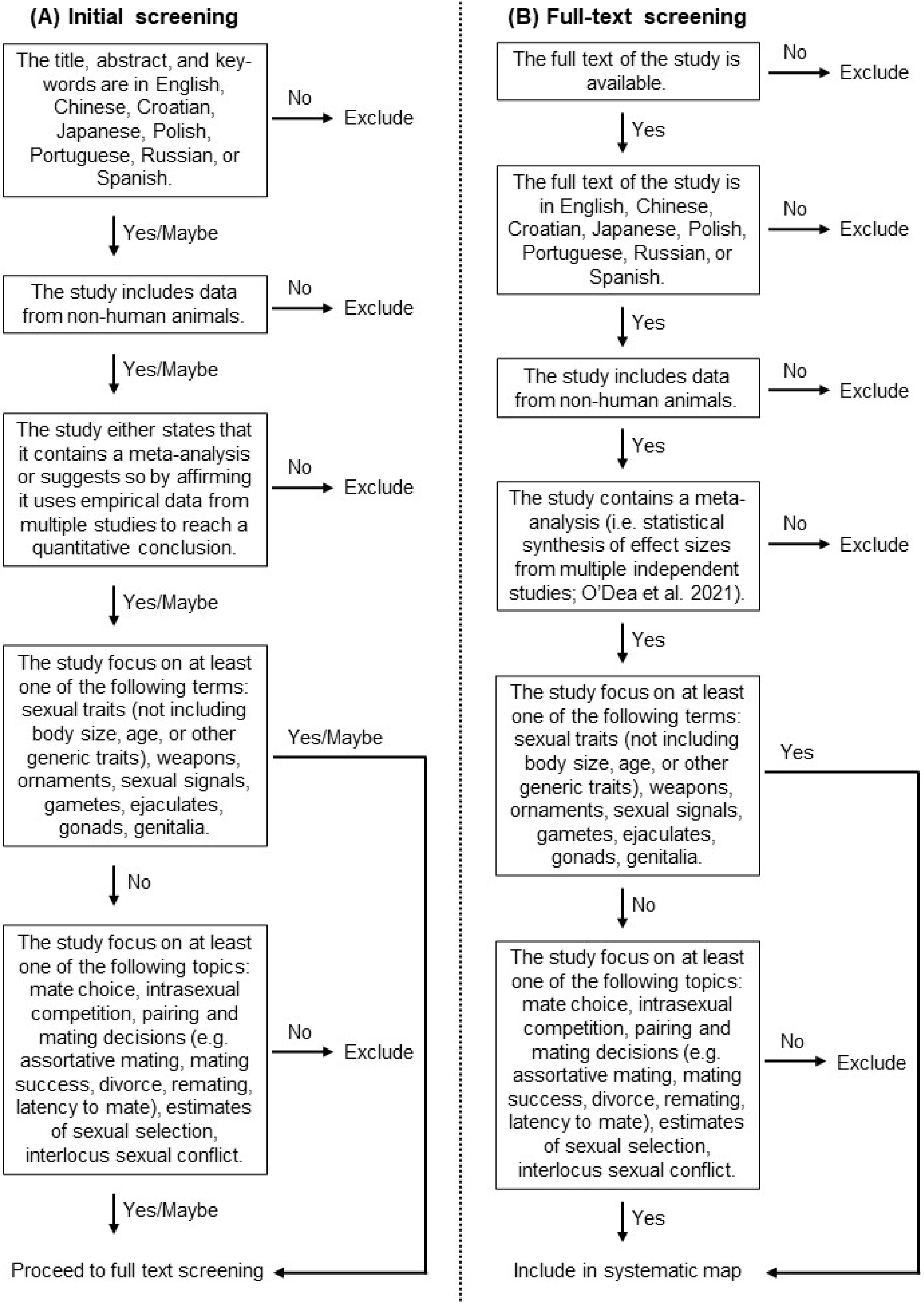
(A) Initial screening
The title, abstract, and key-words are in English, Chinese, Croatian, Japanese, Polish, Portuguese, Russian, or Spanish.
No
Exclude
Yes/Maybe
The study includes data from non-human animals.
No
Exclude
Yes/Maybe
The study either states that it contains a meta-analysis or suggests so by affirming it uses empirical data from multiple studies to reach a quantitative conclusion.
No
Exclude
Yes/Maybe
The study focus on at least one of the following terms: sexual traits (not including body size, age, or other generic traits), weapons, ornaments, sexual signals, gametes, ejaculates, gonads, genitalia.
Yes/Maybe
No
The study focus on at least one of the following topics: mate choice, intrasexual competition, pairing and mating decisions (e.g. assortative mating, mating success, divorce, remating, latency to mate), estimates of sexual selection, interlocus sexual conflict.
No
Exclude
Yes/Maybe
Proceed to full text screening
(B) Full-text screening
The full text of the study is available.
No
Exclude
Yes
The full text of the study is in English, Chinese, Croatian, Japanese, Polish, Portuguese, Russian, or Spanish.
No
Exclude
Yes
The study includes data from non-human animals.
No
Exclude
Yes
The study contains a meta-analysis (i.e. statistical synthesis of effect sizes from multiple independent studies; O'Dea et al. 2021).
No
Exclude
Yes
The study focus on at least one of the following terms: sexual traits (not including body size, age, or other generic traits), weapons, ornaments, sexual signals, gametes, ejaculates, gonads, genitalia.
Yes
No
The study focus on at least one of the following topics: mate choice, intrasexual competition, pairing and mating decisions (e.g. assortative mating, mating success, divorce, remating, latency to mate), estimates of sexual selection, interlocus sexual conflict.
No
Exclude
Yes
Include in systematic map

Figure 1. Decision tree used for literature screening. The initial screening (A) was based on the examination of the title, abstract, and keywords of retrieved studies, while the full text screening (B) was based on the full content of studies that had passed the initial screening.

(3) Data extraction

PP extracted all data from meta-analyses included in our systematic map. Afterwards, YY cross-checked circa 20% of the extracted data to ensure replicability. Details on the extracted variables are provided below.

(a) Systematic map

We extracted data from meta-analytical studies in respect to the scope of their research questions and specific aspects of the data they used regarding taxa, focal sex, and methodological approach. To do this, we used a Google Form questionnaire for each study (Table S3). We modified our initial plan on how to summarise questions from each study to better fit the classification system presented on our systematic map (see section III.2.e). Several aspects made the task of describing and classifying questions from meta-analytical studies complex and subjective (see also section III.5). For instance, not all questions from included studies were relevant to our systematic map, such as questions related to paternal care (e.g. Goldberg *et al.*, 2020). Similarly, not all variables used within certain questions were relevant, such as mating success mixed with other fitness measures (e.g. Leung & Forbes, 1996). Therefore, we selected and described the studies' questions relevant to our systematic map without necessarily relying on the exact words used by their original authors (see further details in Supplementary material, including direct quotes from meta-analyses related to their goals in Table S8). We aimed to extract only questions that we considered central to each meta-analytical study. Because of this, we modified or excluded some variables initially extracted (e.g. how main questions were answered; see also section III.5). Furthermore, when possible, we described studies' questions without mentioning the taxa or sex investigated, as we discuss these issues separately (sections III.2.a and III.2.f). Moreover, we intentionally discussed meta-analyses' questions without mentioning their results to focus on the conceptual and methodological decisions by the authors of these meta-analyses, which is the typical approach of systematic maps (Sutherland & Worldley, 2018).

When possible, we extracted the number of effect sizes, species, and empirical studies used in meta-analyses. We did so by examining both the text and the data from meta-analyses. To improve readability when discussing topics related to sexual selection (section III.2.e), we cite up to five meta-analyses related to patterns we described. If more than five meta-analytical studies were relevant and should have been cited, we instead refer to the Supplementary material where all meta-analytical questions have been described in full. In addition, to avoid repetition, questions that were relevant to multiple topics were omitted from relevant subsections if they had already been mentioned.

One particular piece of information that we collected from meta-analyses was the sex of individuals that were used to calculate effect sizes (discussed in section III.2.f). However, our analysis related to this information was made at the level of the questions extracted from meta-analyses (as in section III.2.e) rather than the meta-analyses themselves. We ultimately classified these meta-analytical questions in relation to the stereotypes represented by the concept of sex roles (following Pollo & Kasumovic, 2022). For instance, meta-analytical questions that focused exclusively on males and their traits were deemed to be "conforming" to the idea of sex roles that poses males as competitive and as the usual sex under sexual selection (Ah-King & Ahnesjö, 2013). Conversely, meta-analytical questions that focused exclusively on females and their traits were “nonconforming” to the idea of sex roles, which poses females as coy (Ah-King & Ahnesjö, 2013). The only exception to this classification was for meta-analytical questions that fitted into the mate choice category (see section III.2.e.4), in which exclusive focus on females was considered conformist, and exclusive focus on males was nonconformist, as the idea of sex roles proposes that females are choosy while males are unselective (Ah-King & Ahnesjö, 2013). Furthermore, meta-analytical questions that focus on both males and females were classified as “neutral”.

(b) Reporting appraisal

We used PRISMA-EcoEvo (O’Dea *et al.*, 2021) to evaluate reporting and methodological aspects of included meta-analyses. Although PRISMA-EcoEvo only provides guidelines and is not an appraisal tool, other appraisal tools (e.g. Woodcock, Pullin & Kaiser, 2014: CEESAT; Shea *et al.*, 2017: AMSTAR 2) do not include items we aimed to quantify. Therefore, we used the PRISMA-EcoEvo checklist for reporting appraisal, choosing a subset of the items that are often deemed key aspects for transparency and robustness of meta-analyses, such as registering planned research (Allen & Mehler, 2019), detailing the search and screening of studies (McGowan *et al.*, 2016; Palpacuer *et al.*, 2019), handling statistical non-independence (Noble *et al.*, 2017), and sharing data (Piccolo & Frampton, 2016), among others (see section III.4). We mainly surveyed whether these elements were described or provided, but for specific aspects we also collected detailed information when possible (e.g. which software was used for statistical inferences). Moreover, although our systematic map included meta-analyses in a broad sense (see section II.2), some may be more restrictive on meta-analyses’ definition (Nakagawa *et al.*, 2023a). Thus, we also verified whether studies included in our systematic map were traditional meta-analyses, i.e. used traditional effect sizes and modelled heterogeneity using additive weighting (Nakagawa *et al.*, 2023a). We primarily assessed this information based on statistical methods described in meta-analyses, including model equations and software used.

(c) Bibliometrics

We extracted affiliations and names of all authors from each meta-analysis. We retrieved this information from Scopus using the packages *bibliometrix* (Aria & Cuccurullo, 2017) and *rscopus* (Muschelli, 2019) in R (R Core Team, 2022), on August 7th and 14th 2023, respectively. We manually extracted this information for studies that were not indexed in Scopus (e.g. theses and recent studies, n = 9). We then determined authors' gender from their first name using the package *genderizeR* (Wais, 2016). Although this approach has its faults (e.g. erroneous label assignment, especially for people that do not identify with binary genders), it includes an estimation of the certainty that a name is associated with a given gender based on real data. Thus, to minimise errors, we only used this automatic labelling when the gender assignment certainty was higher than 95%. For names with ambiguous gender association (i.e. lower certainty), we manually searched the authors' name online to assign gender based on information we could find (e.g. profiles on universities' websites).

(4) Ad-hoc analyses

PP conducted *ad-hoc* analyses (i.e. initially unplanned, thus not in the pre-registration) to further explore our results. We standardised all continuous predictor variables in the models described below to zero mean and then divided by two times its standard deviation (following Gelman, 2008). All analyses were performed in R (R Core Team, 2022).

First, we verified whether the number of species in taxonomically unrestricted meta-analyses was related to the proportion of the two most popular animal groups in their dataset (see section III.2.a). To do so, we conducted Spearman correlations and general linear models (GLMs) with a binomial error structure, weighted by the number of species in each meta-analysis. As this relationship was observed to be non-linear, in addition to analysing all data points together, we also explored the data partitioned into two sets (using an arbitrary value of number of species equal to 70).

Second, we assessed whether meta-analyses with distinct taxonomic scopes included different numbers of species, empirical studies, and effect sizes. We thus performed pairwise comparisons for each of these variables using non-parametric two-tailed Mann-Whitney tests.

Third, we evaluated the relationship between the number of authors and the number of affiliated countries in each meta-analysis. To do this, we conducted a general linear model (GLM) with a Poisson error structure and a Spearman correlation between these variables.

Fourth, we explored whether several aspects regarding authorship diversity were associated with certain biases we found in the secondary literature related to sexual selection. More specifically, we conducted four GLMs with a binomial error structure, each with a different response variable related to meta-analyses': (1) taxonomic scope (unrestricted vs. specific species or animal group; unclear excluded), (2) sex roles conformity (conformist vs. other approaches; unclear excluded), (3) sex roles non-conformity (non-conformist vs. other approaches; unclear excluded) and (4) methodological transparency (using a transparency index; i.e. the sum of values for 11 methodological aspects from our report appraisal divided by the maximum possible sum for each meta-analysis, in which adequate evaluations were transformed to 1, substandard to 0.5, and insufficient to 0; see also section III.4). The second and third response variables are similar but genuinely refer to different elements, i.e.

exclusive use of the conformist sex or of the nonconformist sex (respectively). The latter model used the maximum possible transparency for each meta-analysis as weights because the response variable was a proportion of this number. Although we could have selected more response variables related to our results (e.g. topics related to sexual selection), we believed that these were unfeasible to analyse (e.g. several nominal categories). In each of the GLMs we conducted, we used the following nine predictor variables: (1) binary gender of first author (man vs. woman), (2) proportion of women as authors, (3) number of authors, (4) number of institutions affiliated (including those from the same country), (5) number of countries affiliated, (6) number of continents affiliated, (7) continent of the first affiliation listed (European vs. non-European), (8) proportion of authors from the Global South (see Supplementary material for details), and (9) publication year. We used the function *dredge* from the MuMIn package (Bartoń, 2023) to generate all possible models ($2^9 = 512$ models for each response variable) and select those whose AICc values were less than two units larger than the model with the lowest AICc. We then conducted simplified versions of these GLMs with only predictor variables that appeared in all selected models, i.e. we assumed that only these variables were associated with response variables.

III. RESULTS AND DISCUSSION

(1) Number of eligible meta-analytical studies

Our screening process is summarised in Figure 2. Searches from all sources retrieved a total of 1,215 records, 397 of which were duplicates. We thus assessed the title, abstract, and keywords of the remaining 818 articles, from which 187 met our initial selection criteria (i.e. were initially included). After examining the full-text of these initially included articles, we found that nine of them were duplicates (e.g. theses with published versions already in the dataset), 20 did not meet our broad definition of meta-analysis, seven did not contain a relevant topic to our systematic map, and one was not a formal report (conference extended summary). Therefore, the screening process resulted in the inclusion of 150 records to the systematic map. One of the records (Macedo-Rego, 2020) was a thesis with three relevant chapters (Macedo-Rego, Jennions & Santos, 2020a, 2020b, 2020c), so we counted each of these chapters as distinct studies, tallying 152 studies overall (Figure 3; see also Supplementary material for details on special cases). The first meta-analyses on a topic related to sexual selection was published in the mid-90s, while the increase in their prevalence happened around 2011 (Figure 3).

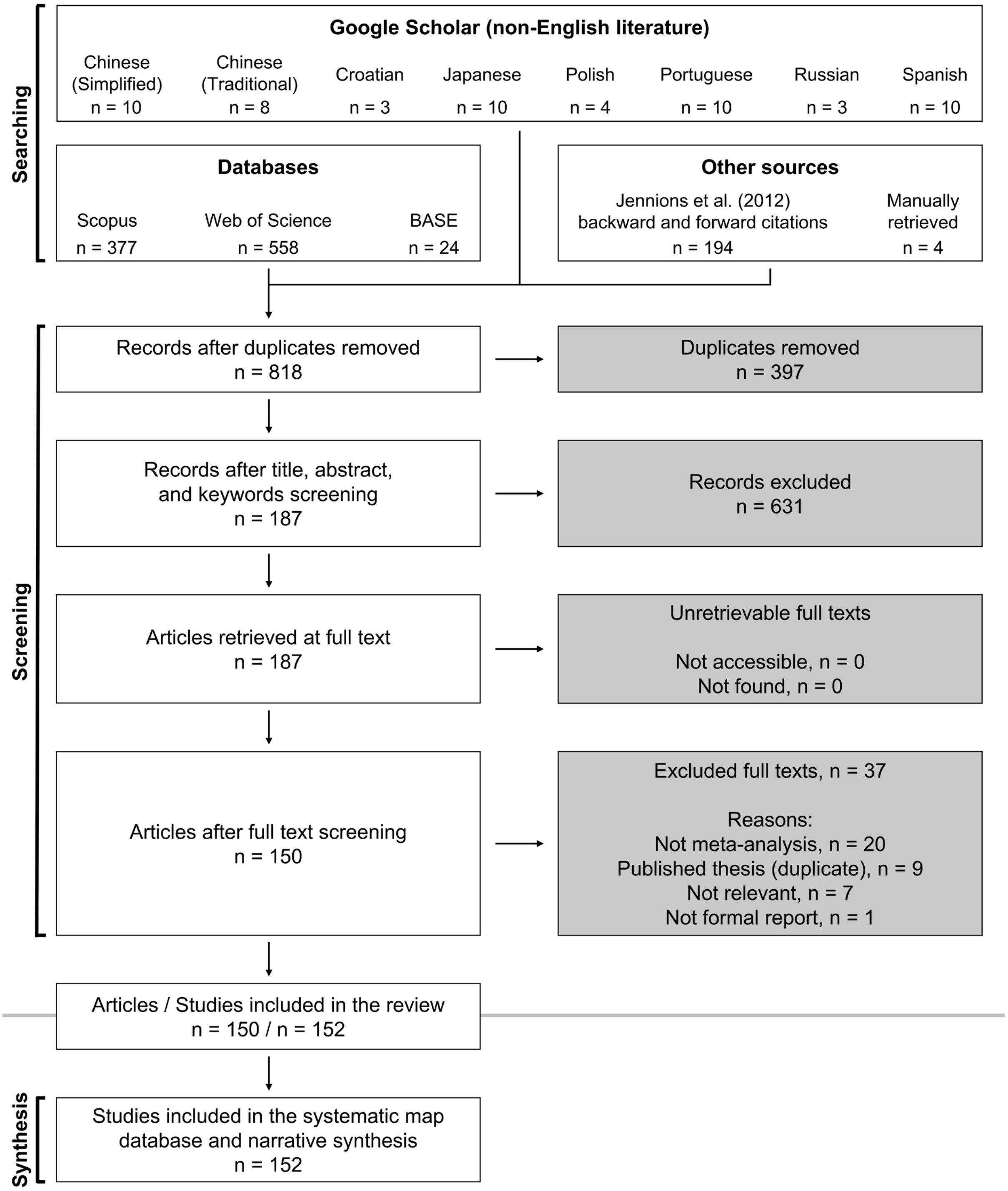

Figure 2. ROSES flow chart of the screening process.

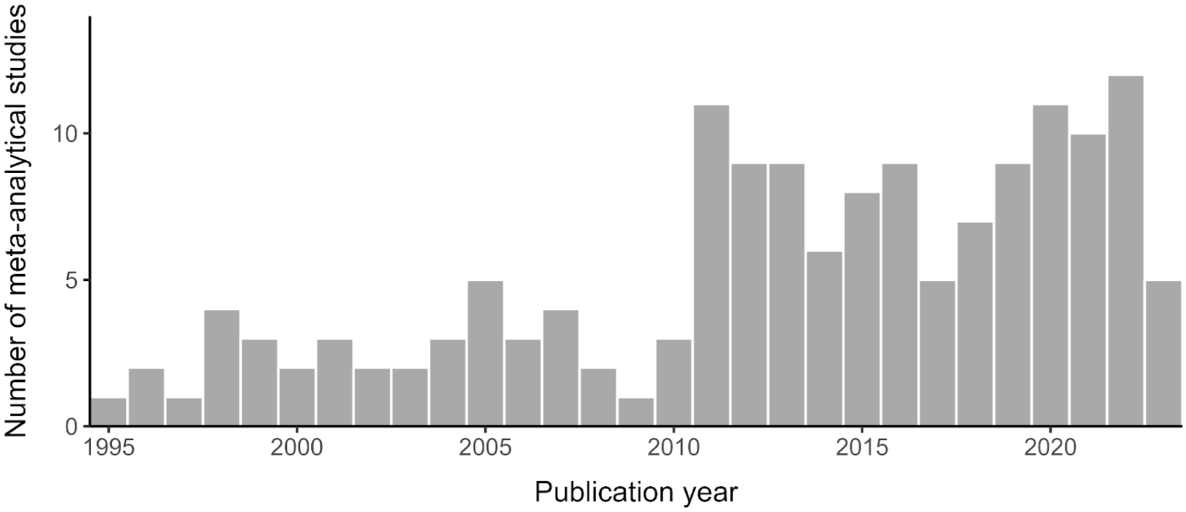

Figure 3. Number of meta-analytical studies on topics related to sexual selection published per year. Our searches were conducted in early 2023 (see section II.1), thus they do not capture publications from the whole year 2023.

(2) Systematic mapping of meta-analyses on topics related to sexual selection

(a) Taxonomic groups

We verified which animal groups (at the taxonomic class level) were synthesised by the meta-analyses included in our systematic map (Figure 4). We found that more than half of all of these meta-analyses (83 out of 152) limited their scope to a single species (14) or to a specific taxonomic group (69), while the remaining ones (69) did not apply taxonomic filters (i.e. all animal species could be included). We then identified the animal groups investigated by these meta-analyses, although we could not obtain relevant details from nine of them. Birds were by far the most popular animal group in our systematic map: 85.7% (12 out of 14) of single species meta-analyses focused on a bird species, 49.3% (34 out of 69) of specific taxonomic group meta-analyses focused exclusively on birds, and half (30 out of 60) of taxonomically unrestricted meta-analyses for which we obtained taxonomic details showed birds as the first or second most copious group in number of species included in these studies

(Figure 4). Insects followed behind, as 14.3% (2 out of 14) of single species meta-analyses focused on an insect species, 18.8% (13 out of 69) of specific taxonomic group meta-analyses focused exclusively on insects, and 80% (48 out of 60) of taxonomically unrestricted meta-analyses for which we obtained taxonomic details showed insects as the first or second most copious group in number of species included in these studies (Figure 4). However, we highlight that the actual proportion of species that first or second most popular animal groups represent in taxonomically unrestricted meta-analyses tends to decrease with the total number of species used by a meta-analysis (Spearman's correlation: $r_s = -0.55$, $p < 0.001$, Figure 5, Table S6). For instance, Soper, Ekroth & Martins (2021) extracted data from nine species in their study, eight of them being insects and one being a mammal, meaning that the two most abundant animal groups in the study represented all its taxonomic diversity. In contrast, Moura *et al.* (2021) included 341 species, 21.1% birds and 20.8% insects, so that these two groups comprised only less than half of the species represented in the study.

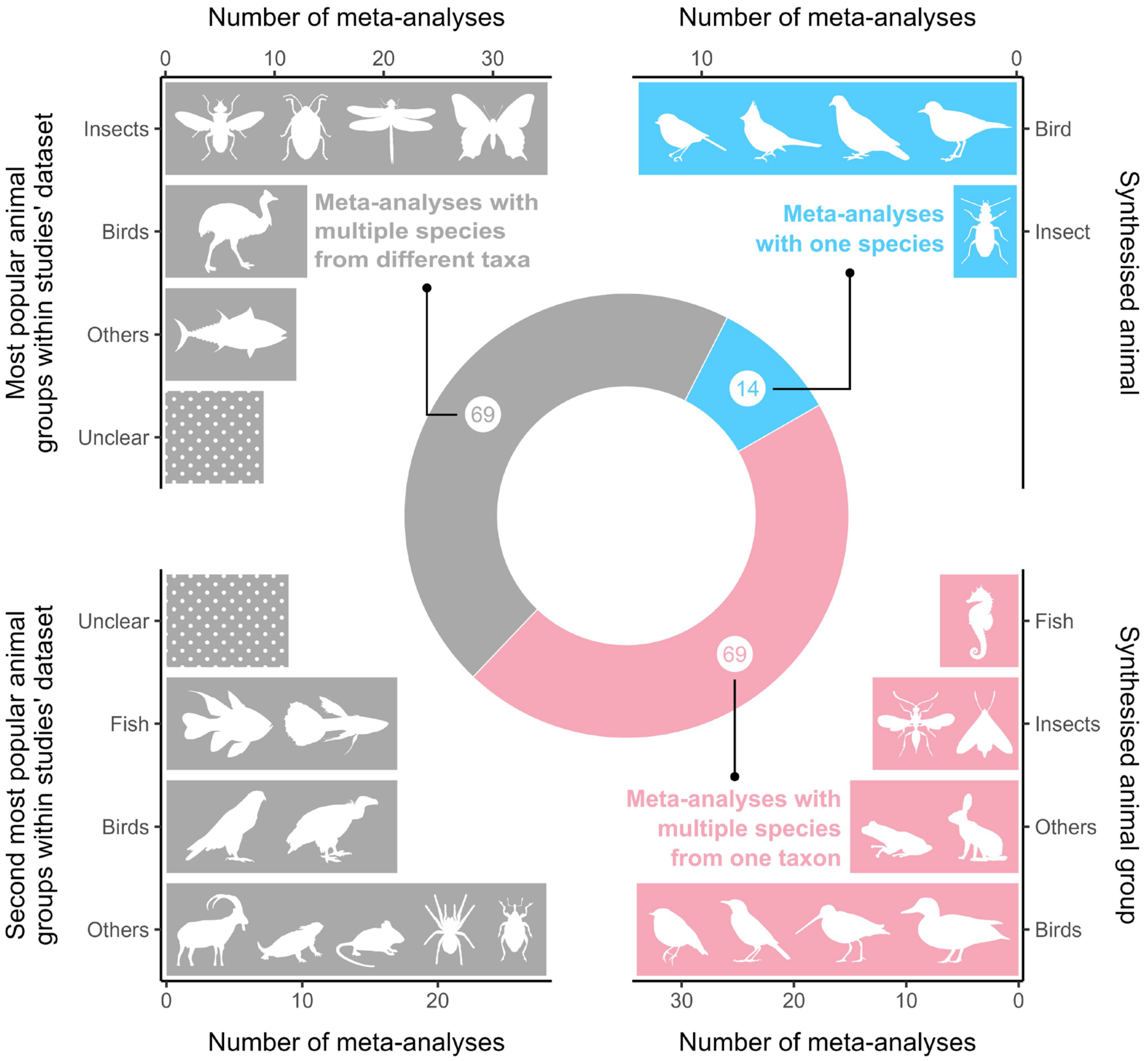

Figure 4. Number of meta-analytical studies related to sexual selection topics per taxonomic scope (centre) and animal groups (bar plots). Animal silhouettes represent broader animal groups and not specific species included in meta-analyses.

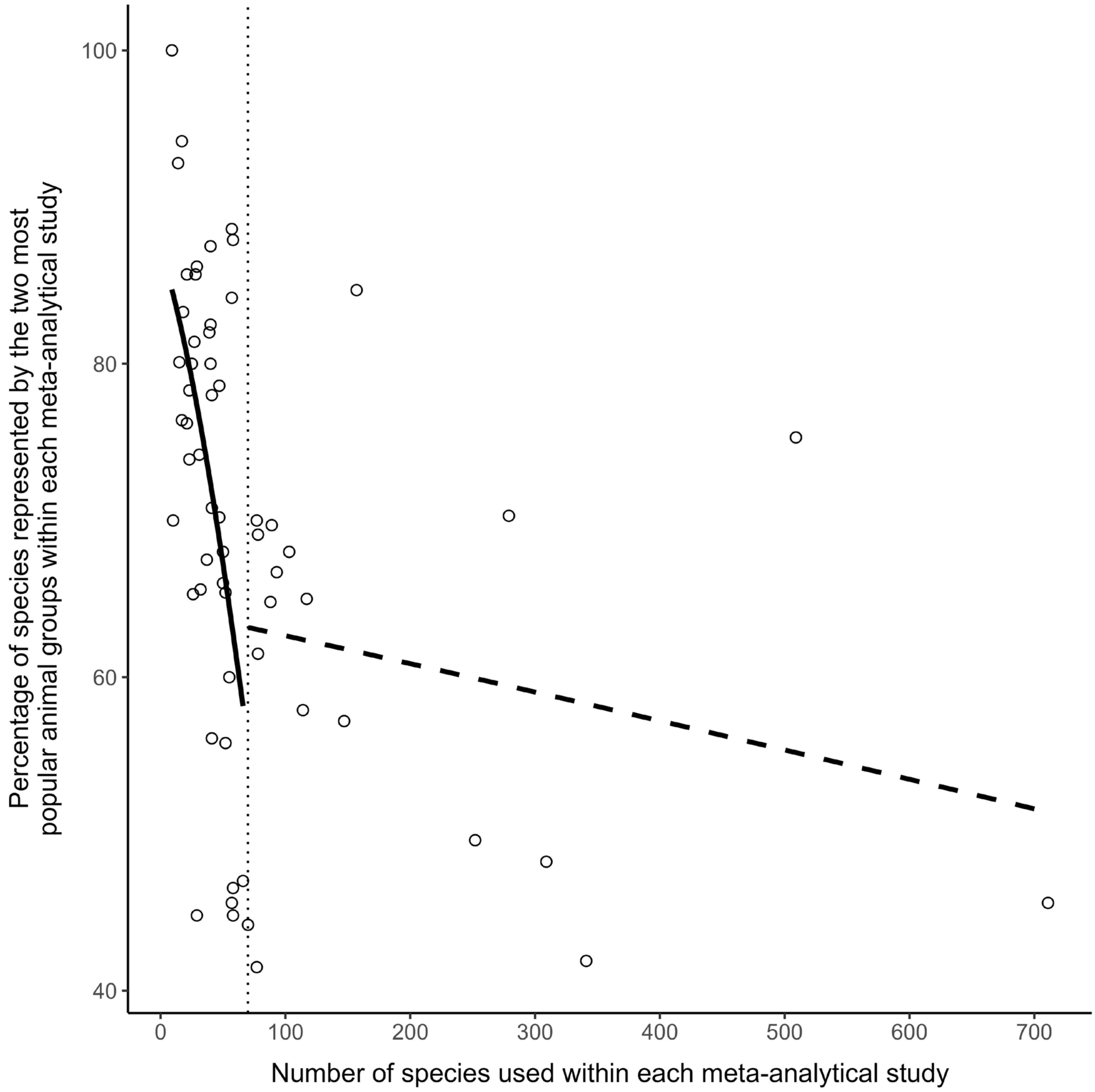

Figure 5. Relationship between the number of species used by meta-analytical studies with multiple species from different animal taxa and the percentage of species represented by the two most abundant animal groups in these studies. The dotted vertical line is an arbitrary number used to separate data into two sets (the first data set contains 41 meta-analyses fewer than 70 species, and the second data set contains 19 meta-analyses with 70 or more species), which makes the non-linear relationship between variables clearer. The solid and the dashed

lines represent the best fit from generalised linear models using the first and second data sets, respectively (Table S6).

Our findings on taxonomical biases are in line with findings of the empirical literature from sexual selection (Zuk *et al.*, 2013), but also from other biological fields and subfields, such as animal behaviour (Rosenthal *et al.*, 2017; see also Owens, 2006), animal ecology (Bonnet, Shine & Lourdais, 2002), parental care (Stahlschmidt, 2011), biodiversity (Troudet *et al.*, 2017), and conservation (Seddon, Soorae & Launay, 2005). Akin to our results, all of these studies found that some taxonomic groups (usually birds) receive much more research attention than others, revealing taxonomic bias. This means that, at least in taxonomically unrestricted meta-analyses, the unequal distribution of data across taxa originates from a bias already present in the primary literature. In addition, our findings represent only the tip of a problematic iceberg, as the sole taxonomic information we extracted from meta-analyses was taxonomic class. As Zuk *et al.* (2013) showed, taxonomic bias is insidious as it occurs at the genus and species level as well. For example, most meta-analyses that include insects have many of their effect sizes from fruit flies (*Drosophila*) and other model species (e.g. de Boer *et al.*, 2021).

Taxonomic bias might stem from distinct sources, such as organisms' conspicuousness and easiness to access (Murray *et al.*, 2015; Yarwood, Weston & Symonds, 2019; Ellison *et al.*, 2021), common human attitudes towards specific animals (e.g. Bjerke & Østdahl, 2004), frequent use of certain organisms for which experimental techniques are well established (i.e. model systems, Zuk *et al.*, 2013), or previous experience with research on a given animal group (Pollo & Kasumovic, 2022). However, accumulating knowledge on only a fraction of the existing animal diversity severely limits our generalisation ability, making this taxonomic hyper focus extremely detrimental to our understanding of natural processes. Assuming that the number of species in a clade increases the variation in traits and patterns (including the ones related to reproduction) observed among its species, we argue that researchers (especially empiricists) should consider the existing diversity of animals when choosing which species to study. While the interest in insects is warranted because this group represents most animal species (Stork, 2018), the same cannot be said about birds, which represent less than 1% of all animal diversity (Zhang, 2013). Following this rationale, we suggest that more attention should be given to invertebrates, especially arthropods, which represent almost 80% of animal species (Zhang, 2013). Unfortunately, little has been done since the first reports of taxonomic bias more than two decades ago (Bonnet *et al.*, 2002), stressing that solutions to this issue (e.g. incentivising research on data deficient animal groups at both low and high taxonomic levels) remain urgent.

(b) Inclusion of humans

Our systematic map deliberately required that meta-analytical studies had to explore non-human animals to be included (see section II.2). Yet, humans could be used along other species in these meta-analyses. We found that 18 studies from our systematic map included humans, albeit this number can be higher given that another three studies were unclear regarding this information. Although this number seems low, it represents almost a quarter of studies (18 out of 75) that did not exclude primates *a priori* (see section III.2.a). Even though mixing humans with other animals in meta-analyses related to sexual selection can be taken as a matter of preference, we discuss the potential issues arising from this decision below.

Darwin’s (1871) book “The descent of man, and selection in relation to sex” addresses human evolution and sexual selection (Ruse, 2015). At times, Darwin (1871) explicitly mixed these topics, using several examples from human society to support his arguments related to sexual selection. Using our own experiences to understand nature is intuitive (Kokko, 2017), and perhaps many scientists believe that studying other animals' reproductive behaviours can help us to comprehend ourselves. However, humans show a distinct aspect from other animals: an extremely complex culture that has a strong effect on our behaviours, including reproduction related behaviours (Eagly & Wood, 1999). For instance, culture influences which phenotypes are deemed attractive (Silverstein *et al.*, 1986) and pair formation can be subjected to the decision of others (e.g. parents' influence; Buunk, Pollet & Dubbs, 2012). Additionally, people may choose to have few or no children through celibacy, contraception methods, or abortion, meaning that reproductive success plainly loses its utility in sexual selection studies when compared with other organisms.

Issues from including humans in meta-analyses of sexual selection are not only problematic for behavioural traits: selection on humans has been modified or even nullified as we increasingly control our environment. For instance, crooked teeth in humans became common only recently, after we started eating processed (soft) foods that relaxed selection for large jaws that could accommodate all of our teeth (Corruccini, 1984; Lieberman *et al.*, 2004). Thus, even for traits that are not under direct influence of culture (e.g. sperm traits), the distinct evolutionary pressures on modern humans might mislead comparisons with other organisms. This argument also applies for domesticated animals, as the process of artificial selection applied on them can modify their traits, as noted by Mautz *et al.* (2013).

We advise evolutionary biologists to avoid mixing humans with other animals in meta-analyses on topics related to sexual selection for the reasons above. Although humans are simply another animal species, equating processes and patterns of non-human organisms to the ones seen in modern humans can lead to anthropomorphisation of other organisms.

This might be especially relevant for how we think of males and females (and their reproductive patterns; see section III.2.f), as our gender notions may affect our perceptions of them (Ahnesjö *et al.*, 2020; Pollo & Kasumovic, 2022). For example, Darwin (1871) argued that women are inferior to men, among other conclusions based on his observations from the Victorian society he lived in, which were described as processes emerging from our biology. A potential consequence of this type of rationale is falling into a vortex of self-affirmation, in which our societal views influence our notion of sex differences in nature and *vice versa*. In fact, a part of evolutionary psychology, a field born out of evolutionary biology from the 1970s (strongly based on Trivers, 1972; see also Fausto-Sterling *et al.*, 1997), seems to have succumbed to this pattern as it recurrently overemphasises gender differences (Eagly & Wood, 1999; Stewart-Williams & Thomas, 2013). Studies from evolutionary psychologists commonly rely on assumptions related to other animals and ancestral human societies (for which information is scarce and biased, see Anderson et al., 2023; Lacy & Ocobock, 2023) to make hypotheses on current human behaviours (e.g. Geary, 2021). For instance, Lewis *et al.* (2017) claimed that high-heels make women more attractive because they can increase women's lumbar curvature, representing a morphological adaptation for child bearing that would ultimately signal their high-quality to men. Lewis *et al.* (2017), however, barely mentioned alternative non-biological explanations to why women are deemed more attractive in high heels (e.g. influence of media). In addition, the authors completely ignored any historical relevant facts about high-heels, including that they were also used by men and were a symbol of masculinity for seven centuries before being associated with femininity in the 18th century (Semmelhack, 2020). This shows that reducing human behaviours to a simple biological product, which is an assumption implicitly made by meta-analyses related to sexual selection that include them with other species, can have profound consequences. If researchers strongly disagree with our stance of excluding humans from meta-analyses with other animals, we suggest that they at least include additional analyses, in which effect sizes obtained from humans are analysed separately to assess their role in the study's conclusions (e.g. with a moderator that compares humans with non-human animals; as in Fromonteil *et al.*, 2023).

(c) Number of empirical studies, effect sizes, and species

We found that the number of empirical studies, effect sizes, and species generally increased with taxonomic scope (Figure 6, Table S7). Along with taxonomic distribution of the data, these numbers are pivotal to address generality limitations in meta-analyses (Spake *et al.*, 2022). However, they are rarely provided in-text. For instance, although Cally, Stuart-Fox & Holman (2019) used a total of 459 effect sizes from 65 empirical studies (both numbers mentioned in-text), these were related to only 15 species. Yet, the authors did not mention this low number of species and did not discuss the impacts of relying on such a limited taxonomic dataset to make a statement for the entire animal kingdom. This often appears as a symptom of a neoliberal academia (Lorenz, 2012), which pushes researchers to publish in high impact factor journals that require bold claims, stimulating the concealment of weaknesses to increase significance.

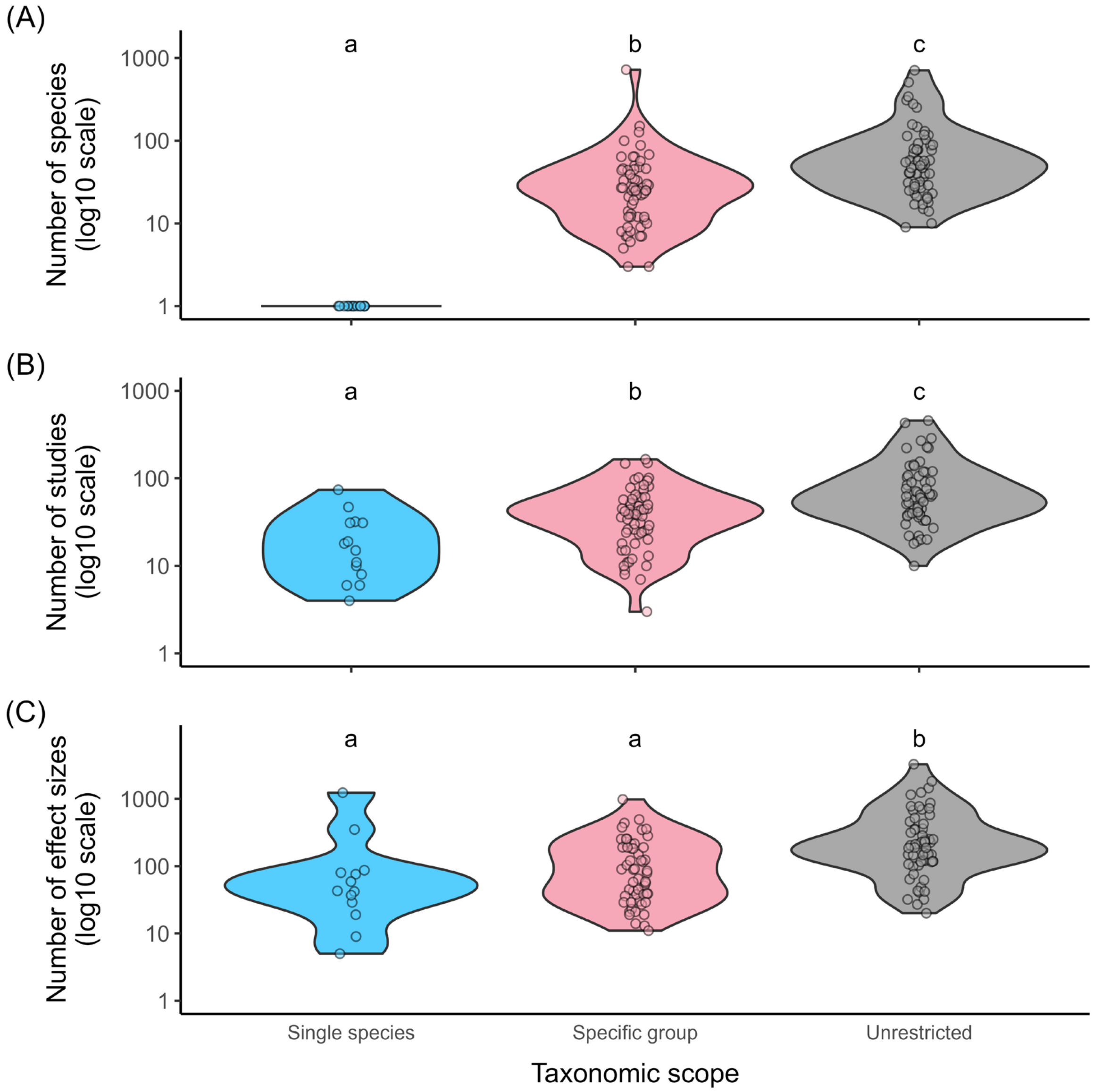

Figure 6. Number of effect sizes (A), species (B), and empirical studies (C) found in meta-analytical studies (logarithmic scale) on topics related to sexual selection depending on their taxonomic scope. Distinct letters within each plot indicate statistical differences among taxonomic scopes for each variable (Table S7).

(d) Study design

Briefly stating the design employed by selected empirical studies (experiments or field observations) represents the bare minimum of transparency from meta-analyses. Yet, we found that almost 40% (60 out of 152) of the meta-analytical studies from our systematic map were unclear about this information. From those that specified this information (92), 13 exclusively used field observations, 32 exclusively used experimental investigations, while 47 combined both designs. A comprehensive description of included studies' methodology is ideal as it helps meta-analyses' readers to identify some of their limitations (Page *et al.*, 2021). This is because observations and experiments can have multiple peculiarities and vary in the degree of variables controlled, especially when distinct organisms require methodological adjustments. The design type selected by a meta-analysis has direct impacts on what is in fact being evaluated. For instance, to attest mate choice one needs to isolate several variables (e.g. number of individuals present; see section III.2.e.4), so field observations are much less reliable. Mixing approaches is fine if authors use moderators to distinguish one design from another (e.g. mate choice experiments vs. mating success observations), which is a missing aspect in some meta-analyses in the field of sexual selection (e.g. Møller & Jennions, 2001; Ord & Stamps, 2009).

(e) Topics related to sexual selection

We extracted a single research question from 85% of meta-analytical studies (129 out of 152) and two to four research questions from the remaining 15% (23), resulting in a total of 187 research questions. Figure 7 illustrates the number of questions in each of the categories (i.e. topics connected to sexual selection) we created to classify meta-analytical questions: (1) pre-copulatory sexual traits, (2) pre-copulatory intrasexual competition, (3) post-copulatory intrasexual competition, (4) mate choice, (5) remating and eagerness to mate, (6) mating success, (7) mating patterns, (8) divorce and extra-pair patterns, and (9) sexual conflict and estimates of sexual selection. We assigned up to two topics we deemed most relevant to individual questions rather than to meta-analyses (but see Supplementary material). This resulted in 138 questions associated with a single topic and 49 associated with two topics (visualised as links between categories in Figure 7). Details of what each category within our classification framework encompass are discussed below.

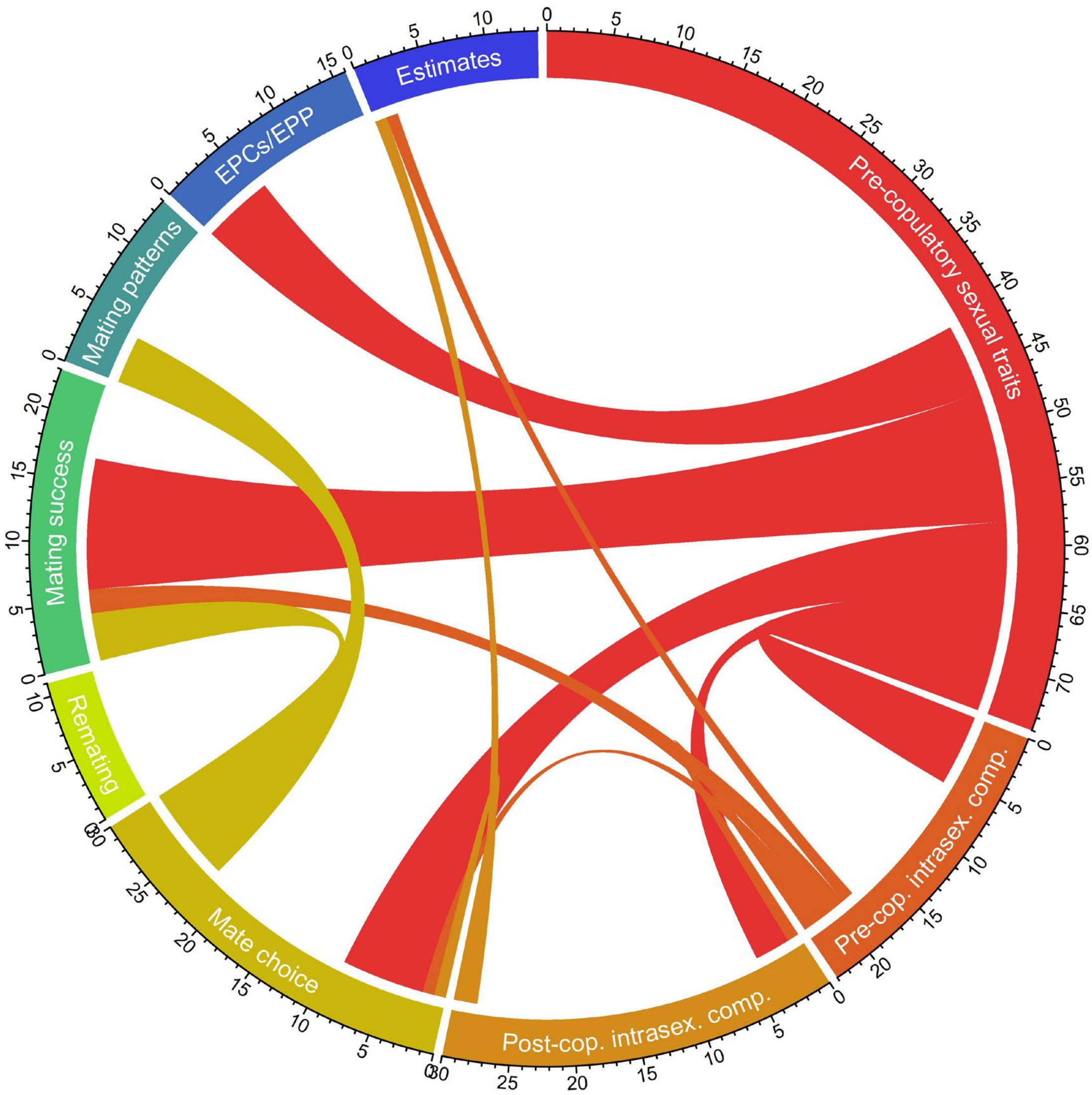

Figure 7. Number of meta-analytical questions for each topic related to sexual selection. Links represent questions that fit into two topics. Topics (clockwise, red to blue): pre-copulatory sexual traits, pre-copulatory intrasexual competition and associated traits, post-copulatory intrasexual competition and associated traits, mate choice, remating and eagerness to mate, mating success, mating patterns, divorce and extra-pair patterns (EPCs/EPP), sexual conflict and estimates of sexual selection.

(1) Pre-copulatory sexual traits

This category of our classification framework includes questions explicitly mentioning pre-copulatory sexual traits, such as secondary sexual characteristics, ornaments, courtship, and sexual signals. Although weapons would technically fit here (see section III.3.b), we noticed that a distinct set of meta-analyses focused on them, so we classified them differently (see section III.2.e.2). However, we note that some meta-analyses grouped several different traits under a single label (e.g. secondary sexual traits), and weapons might be inadvertently amongst them. In total, this category encompassed 74 questions from 59 meta-analytical studies, revealing this topic as the most popular in the meta-analytical literature related to sexual selection (Figure 7).

The emphasis on pre-copulatory sexual traits is expected, as Darwin (1871) himself used them to develop the theory of sexual selection (see section III.3.b). He proposed that ornaments and sexual signals evolved via mate choice, an idea that was rejected by his peers at the time (Hoquet & Lewandowsky, 2015). Nonetheless, the literature on ornaments and sexual signals later flourished with a debate among evolutionary biologists: whether these traits and signals evolved because they reflect greater genetic quality to prospective mates ("good genes" model and its "handicap principle" extension; Zahavi, 1975, 1977) or simply because they genetically correlate with mate preference for themselves (i.e. Fisherian runaway process; Fisher, 1930; see also Eshel, Volovik & Sansone, 2000; Kokko, 2001; Hoquet & Lewandowsky, 2015). Possibly because the latter is complex and difficult to measure (but see Greenfield *et al.*, 2014), the former has received much more empirical attention.

On one hand, some proponents of the good genes model (e.g. Andersson, 1994) predicted that ornaments and sexual signals would be linked to fitness-impacting measures (e.g. survival, fecundity, viability, overall reproductive success; see Kokko, 2001), which was tested by many different meta-analyses (Table S8). On the other hand, Grafen (1990a, 1990b) popularised Zahavi's (1975, 1977) idea that ornaments and sexual signals must be condition-dependent to be honest (reviewed and contested in Penn & Számadó, 2020; see also Getty, 2006), shifting the attention of the research community to more direct questions. It is unsurprising then that 26 meta-analyses in our systematic map contain at least one question asking whether the expression of ornaments and sexual signals is related to the expression of other traits (e.g. age, body size) or to proxies of individual quality (e.g. parasite load; or their manipulation, e.g. diet supplementation, stress) (Table S8). Questions of this nature do not aim to test whether pre-copulatory sexual traits are indeed under sexual selection, but simply whether they function as reliable cues of good genes to prospective mates.

Conversely, a variety of meta-analytical studies (18) tested whether certain ornaments and sexual signals might be under selection by verifying their relationship with intrasexual competition (e.g. dominance rank or aggression; Nakagawa *et al.*, 2007; Yasukawa *et al.*, 2010; Santos, Scheck & Nakagawa, 2011; Parker, 2013; Sánchez-Tójar *et al.*, 2018), species recognition (Ord & Stamps, 2009; Ord, King & Young, 2011; Parker *et al.*, 2018), attractiveness in mate choice experiments (Parker & Ligon, 2003; Simons & Verhulst, 2011;

Hernández *et al.*, 2021), mating success, or extra-pair patterns (Table S8). Other meta-analytical studies explored whether courtship behaviours, ornaments, and/or sexual signals are related to specific biotic (e.g. density, predation, etc; Weir, Grant & Hutchings, 2011; De Jong *et al.*, 2012; Dougherty, 2021a; White, Latty & Umbers, 2022) and abiotic conditions (e.g. habitat structure, band colouration, etc; Boncoraglio & Saino, 2007; Seguin & Forstmeier, 2012; Parris & McCarthy, 2013). At last, other specific meta-analytical studies assessed sexual traits' additive genetic variation (Pomiankowski & Møller, 1995) and heritability (Prokop *et al.*, 2012; Prokuda & Roff, 2014), compared the allometry of sexual traits depending on their function and denomination (Voje, 2016; Rodríguez & Eberhard, 2019), verified whether pre-copulatory sexual traits are associated with sperm quality (Mautz, Møller & Jennions, 2013), examined the interplay between call length and reply latency across species (Bailey & Hammond, 2003), and evaluated the association between expression of possibly sexually selected traits and speciation rates (Kraaijeveld, Kraaijeveld-Smit & Maan, 2011).

We found that most meta-analytical questions related to pre-copulatory sexual traits explored only visual and/or acoustic characteristics (Figure 8; Table S9). In addition, some meta-analyses were unclear on the exact traits used (see also section III.3.b). We observed only nine meta-analytical studies with a question focusing on pre-copulatory sexual traits from other modalities (Figure 8; Table S9). Yet, even in these studies, visual and acoustic traits predominate over others, revealing that some sensory modalities (e.g. olfactory, tactile) are neglected. We discuss the implications of this pattern in section III.3.b.

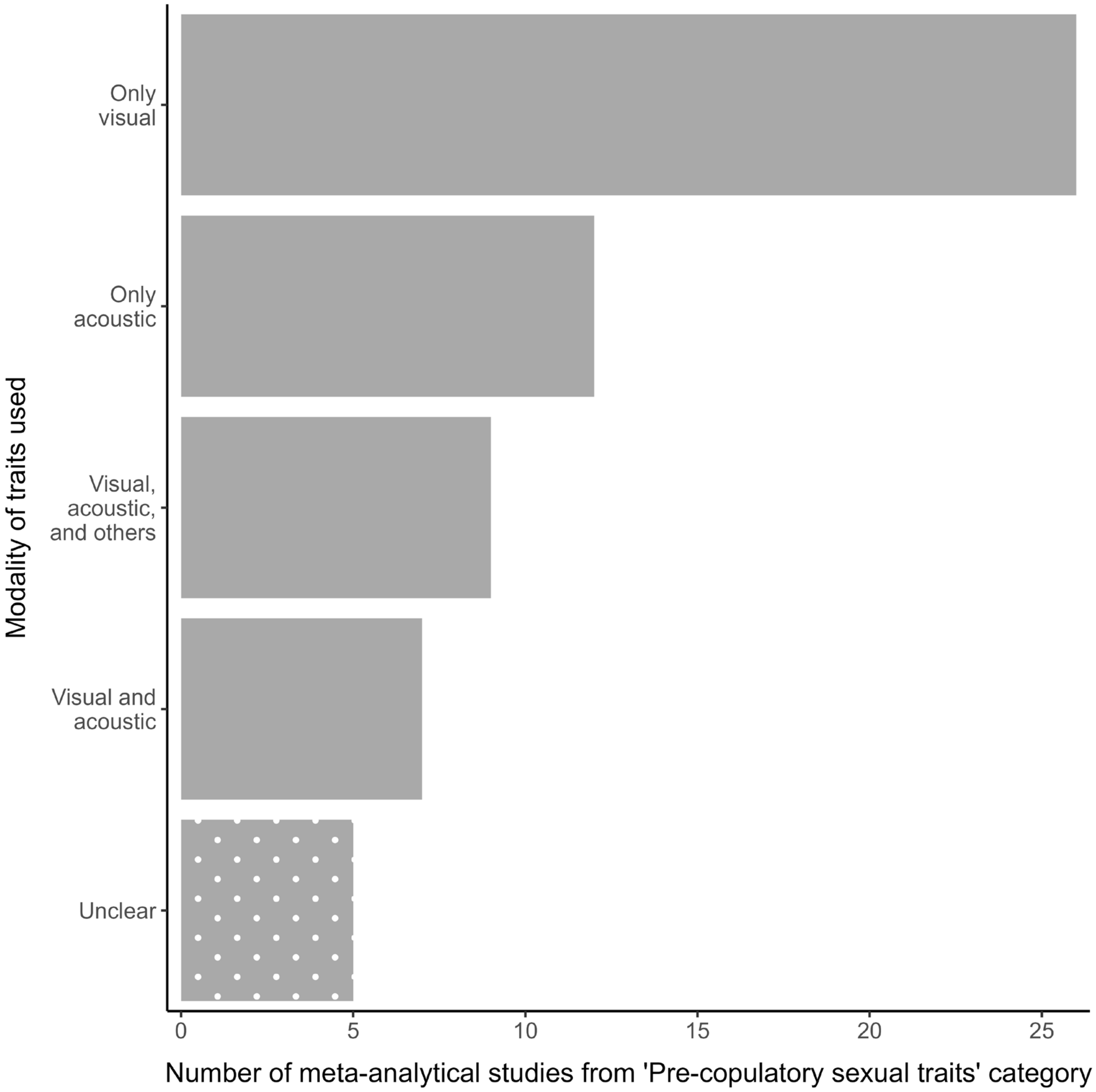

Figure 8. Sensory modality of traits nominated as secondary sexual characteristics, ornaments, or sexual signals from meta-analyses with at least one question categorised as “Pre-copulatory sexual traits”. Visual traits include colour, morphology, and visual displays.

(2) Pre-copulatory intrasexual competition and associated traits

Pre-copulatory intrasexual competition refers to the competition among individuals of the same sex for access to individuals of the opposite sex (Darwin, 1871; Andersson, 1994). This process and its strength as an evolutionary force was fairly accepted by the scientific community when Darwin (1871) shared this idea (Hoquet & Lewandowsky, 2015). Pre-copulatory intrasexual competition includes intrasexual aggression, dominance, mate monopolisation, territoriality, and weaponry, which are subjects covered in this section. Perhaps precisely because this mechanism is perceived as straightforward, relatively few questions explicitly focus on this topic in meta-analyses: only 23 questions from 22 studies were included in this category of our systematic map (Figure 7; see also McCullough *et al.*, 2016).

Animal weapons represent the heartthrob of intrasexual competition as these traits are pivotal for intrasexual combat as well as for assessment signalling to avoid physical confrontations in many species (Emlen, 2008; Rico-Guevara & Hurme, 2019). A couple of meta-analyses tested a key assumption related to these traits: whether weapons are indeed related to contest success (Vieira & Peixoto, 2013; Palaoro & Peixoto, 2022; although the first used resource holding potential, which included other traits). Similarly, Kelly (2008) examined the relationship between resource holding potential (considering weapons and other traits), resource value, and reproductive success. Furthermore, some authors explored whether expression of weaponry is associated with certain contexts, such as the type of disputed resource (e.g. mates vs. territory; Maciel, Oliveira & Peixoto, 2023) or the availability of reproductive sites (Alissa, 2018). Moreover, Menezes & Palaoro (2022) investigated whether size and number of spurs are associated with body and wing size, which are traits connected to flight capacity. Lastly, Lüpold *et al.* (2015) verified whether the expression of weapons is linked to sperm length, whereas Rodríguez & Eberhard (2019) compared allometry slopes of weapons with those of ornaments.

As previously mentioned, some studies evaluated whether ornaments are linked to aggression or dominance (Nakagawa *et al.*, 2007; Yasukawa *et al.*, 2010; Santos *et al.*, 2011; Parker, 2013; Sánchez-Tójar *et al.*, 2018). In respect to territoriality, Ord (2021) assessed the costs associated with this behaviour whilst Ord *et al.* (2011) verified whether species recognition occurs for territorial signals. Other meta-analytical investigations explored whether different contexts and conditions are associated with the expression and intensity of intrasexual competition, such as operational sex ratio (Weir *et al.*, 2011), environmental stability (Peixoto, Medina & Mendoza-Cuenca, 2014), and availability of reproductive sites (Alissa, 2018). Finally, certain meta-analyses attempted to answer questions involving other topics by examining the following relationships: mating success and fighting frequency (Fiske, Rintamaki & Karvonen, 1998) or social dominance (Majolo *et al.*, 2012), strength of mate choice and traits determinant to intrasexual competition success or attractiveness (Pollo *et al.*, 2022), and mate monopolisation and estimates of sexual selection (Macedo-Rego *et al.*, 2020b) or the effect of body size on reproductive success (Macedo-Rego *et al.*, 2020c).

(3) Post-copulatory intrasexual competition and associated traits

Post-copulatory intrasexual competition, popularly known as sperm competition, occurs when ejaculates from different males compete for a set of ova (Parker, 1970; Parker & Pizzari, 2010). Darwin (1871) did not know this was possible, so this subject emerged much later than pre-copulatory processes in the literature of sexual selection. In this category, we gathered 30 meta-analytical questions (from 27 studies) involving gamete traits, ejaculate traits, primary sexual characteristics (i.e. traits necessary for reproduction, e.g. gonads and genitalia, see section III.6.b), risk and intensity of sperm competition, as well as paternity protection behaviours (e.g. mate guarding) (Figure 7).

Most questions in this category concentrated on the expression of gametes, ejaculates, and/or primary sexual traits. For example, several meta-analyses investigated the relationship between these traits, their allocation, or their production, and either (1) another type of trait (e.g. alternative reproductive tactics: Aguiar Del Matto, 2018; Dougherty *et al.*, 2022; body size or mass: Hayward & Gillooly, 2011; Lüpold & Fitzpatrick, 2015; Kim *et al.*, 2021; mating status: Zhang *et al.*, 2016; secondary sexual traits: Mautz *et al.*, 2013; weapons: Lüpold *et al.*, 2015), (2) a specific context (e.g. contaminants: Marmol, 2022; diet or nutrient intake: Crean & Senior, 2019; Macartney *et al.*, 2019; inbreeding: Losdat, Chang & Reid, 2014; masculinization: Senior, Johnson & Nakagawa, 2016b; mate quality: Kelly & Jennions, 2011; presence of ovarian fluid: Myers *et al.*, 2020; presence of rivals: delBarco-Trillo, 2011; Kelly & Jennions, 2011; sexual cannibalism: Dharmarathne & Herberstein, 2022; temperature: García-Roa *et al.*, 2020), or (3) a potential consequence (e.g. allometry patterns: Voje, 2016; patterns of sperm competition risk: Lüpold *et al.*, 2020; trait selection: Dougherty & Shuker, 2016; speciation rates: Kraaijeveld *et al.*, 2011). In addition, some studies evaluated the relationship between two gamete traits (e.g. Bernasconi & Hellriegel, 2005) or between a gamete trait and a primary sexual trait (especially gonad mass; e.g. Joly & Schiffer, 2010; Lüpold & Fitzpatrick, 2015; Lüpold *et al.*, 2015). The remaining questions that fit this category explored the connection between mate guarding and operational sex ratio (Weir *et al.*, 2011), individual quality, or paternity (Harts *et al.*, 2016); copula duration and sperm transfer (Dharmarathne & Herberstein, 2022) or operational sex ratio (Weir *et al.*, 2011); and diverse measures of sperm competition and availability of reproductive sites (Alissa, 2018).

(4) Mate choice

Mate choice is also known as intersexual competition, but some researchers advise to avoid this term (e.g. Andersson, 2021; Shuker & Kvarnemo, 2021a, 2021b). This is because mate choice consists of competition among individuals of the same sex in which individuals of the opposite sex act as mediators, not competition between the sexes as the term intersexual competition seems to suggest (Andersson, 2021; Shuker & Kvarnemo, 2021a, 2021b). Regardless of its denomination, mate choice is commonly thought as acceptance (or rejection) of individuals of certain phenotypes by individuals of the opposite sex, leading to non-random mating (Halliday, 1983). However, any investment dependent on prospective or realised mates' phenotype before, during, and/or after copula, can be considered mate choice (Bonduriansky, 2001; Edward, 2015). This means that both males and females can express mating preferences inconspicuously by, for example, adjusting courtship effort or sperm allocation depending on a mate's phenotype (Reinhold, Kurtz & Engqvist, 2002), or even selecting gametes from particular individuals inside their reproductive tract (i.e. cryptic choice; Thornhill, 1983; Eberhard, 1996, 2019; Firman *et al.*, 2017). Here, we discuss meta-analytical questions that claim to investigate mate choice or mate attractiveness (but see Supplementary material), even though some of them might also include measures that confound with other topics (see below). In total, this category included 30 questions from 29 studies (Figure 7).

Despite the many ways organisms can express mate preferences, assessing mate choice represents a challenge as decisions of individuals of both sexes are often involved (reviewed in Dougherty, 2020). Consider the outcome of an experiment in which a male and a female are put together in a confined space: if they copulate, was it a product of choice or coercion? If they do not, who was responsible for the rejection? The male, the female, or both? As if the confusion from this simple scenario is not concerning enough, several meta-analytical studies combine mate choice experiment outcomes with observations from the field or of mixed groups of individuals regarding individuals' mating success (e.g. Møller & Thornhill, 1998; McLean, Bishop & Nakagawa, 2012; Kamiya *et al.*, 2014; Dougherty, 2023) or mating patterns (e.g. Yukilevich, 2012; Ihle & Forstmeier, 2013; Winternitz *et al.*, 2017; Rometsch, Torres-Dowdall & Meyer, 2020), which can be a product of other processes besides mate choice (see sections III.2.e.6 and III.2.e.7).

Most questions that fit the mate choice category are simply concerned with identifying which aspects or traits are preferred by mates (Table S8). In contrast, other studies attempt to understand the conditions that modulate the strength and/or direction of mate choice expression (e.g. choosers' traits: Pollo *et al.*, 2022; Dougherty, 2023; Richardson & Zuk, 2023; experimental design: Dougherty & Shuker, 2015; conspecifics' choices: Jones & DuVal, 2019; Davies *et al.*, 2020; temperature: Pilakouta & Baillet, 2022; various: Dougherty, 2021b). Although we note that species or population recognition might be a distinct process to mate choice (Rosenthal, 2017), five meta-analyses we included here explored whether individuals prefer conspecifics over others from different populations or species (Ord & Stamps, 2009; Ord *et al.*, 2011; Yukilevich, 2012; Parker *et al.*, 2018; Rometsch *et al.*, 2020). Lastly, other meta-analyses in this category evaluated the heritability of mate preferences (Prokuda & Roff, 2014) and the covariance between mate choice and preferred traits (Greenfield *et al.*, 2014).

(5) Remating and eagerness to mate

In this category, we combined other reproductive aspects that have not yet been covered in the topics already discussed above: remating and eagerness to mate. While these are thought of as simple cogs in the reproduction machine and not as mechanisms of sexual selection, they can still be crucial to sexual selection. For example, when females of species with internal fertilisation mate more than once (i.e. are polyandrous), male-male competition may also occur post-copula through sperm competition, affecting sexual selection on males (Parker & Pizzari, 2010; Kvarnemo & Simmons, 2013). Despite the importance of examining factors related to remating and eagerness to mate, we detected only 11 questions (each from a different meta-analysis) that fitted this category (Figure 7).

The majority of the questions from this topic are alike: they evaluate the benefits and/or costs to individuals (or to their offspring) of mating multiple times versus mating once or fewer times (Table S8). Similarly, two other studies verified whether individuals' mating history can influence the available resources they have for further copulas, as well as their subsequent impact on the reproductive success of individuals they copulate with (Torres-Vila & Jennions, 2005; Zhang *et al.*, 2016), which ultimately could influence remating decisions. The remaining studies in this category are slightly distinct: Mori & Evenden (2013) investigated the association between delayed mating and fitness, while Pilakouta & Baillet (2022) assessed whether eagerness to mate is related to temperature.

(6) Mating success

Until now, we have mostly discussed proximate topics that involve individual traits and decisions, from morphological structures to complex sets of behaviours. Yet, sexual selection (and evolution of sexual traits) only occurs when intrasexual competition and mate choice produce variation in individuals' fitness. Darwin (1871) proposed that this occurs when these mechanisms produce skewed mating success, in which only a portion of the best competitors (through force or looks) mate and leave descendants (but see section III.2.e.9). We found a total of 23 questions focusing on mating success, from 21 meta-analyses (Figure 7). Most of these questions are related to sexual traits and mechanisms of sexual selection, which have already been discussed in previous topics (see above). Other questions in this category explore whether mating success is linked to body size (e.g. Sokolovska, Rowe & Johansson, 2000; Kim *et al.*, 2021) or to specific conditions (e.g. density and sex ratio: Nieberding & Holveck, 2017; lek size: Isvaran & Ponkshe, 2013; parasitism: Hasik & Siepielski, 2022; temperature: Pilakouta & Baillet, 2022).

(7) Mating patterns

While mating success refers to the number of mates obtained, mating patterns arise from the phenotypes of males and females observed together (i.e. in copula or in social pairs). Non-random mating patterns are referred to as assortative or disassortative mating, meaning that individuals within pairs are more similar or dissimilar to one another than expected by chance, respectively. Thus, all 14 meta-analytical questions (each from a different study) that fitted this category (Figure 7) explicitly mention assortative or disassortative mating. Mating patterns can be influenced by different elements, from mechanisms of sexual selection (intrasexual competition and mate choice) to temporal or spatial segregation (Jiang, Bolnick & Kirkpatrick, 2013). This means that studies on mating patterns usually concentrate on what is observed (often in the field), not necessarily how these patterns arise.

Many questions from this topic investigated whether non-random mating patterns occur in respect to a specific trait, such as body size (Arnqvist *et al.*, 1996; Graham *et al.*, 2015; Green, 2019), relatedness (Ihle & Forstmeier, 2013; Pike, Cornwallis & Griffin, 2021), major histocompatibility complex (Winternitz *et al.*, 2017), or population or species identity (Randler, 2008; Rometsch *et al.*, 2020; with some specifically testing population isolation on reproductive isolation: Florin & Ödeen, 2002; Yukilevich, 2012). Conversely, other questions were unrestricted regarding traits evaluated (e.g. Jiang *et al.*, 2013; Janicke *et al.*, 2019; Wang *et al.*, 2019; Moura *et al.*, 2021), with some of them assessing whether observer bias (Wang *et al.*, 2019) and sample pooling methods (Moura *et al.*, 2021) were associated with estimates observed. Lastly, Janicke *et al.* (2019) verified whether assortative mating is related to species richness.

(8) Divorce and extra-pair patterns

All topics discussed so far are relevant for the entire animal kingdom (although taxa are unequally investigated, see section III.2.a). Here, however, we discuss divorce, extra-pair copulations (hereby EPCs), and extra-pair paternity (hereby EPP), which pertain to a specific niche in the sexual selection literature that applies only to socially monogamous animals (forming exclusive social pairs for reproduction). In this context, divorce means re-pairing with another individual whilst the previous partner is still alive (Choudhury, 1995), whereas EPP refers to fertilizations from EPCs (i.e. copulas outside of the social bond; Griffith, Owens & Thuman, 2002). Altogether, this category gathered 16 questions from 16 meta-analyses (Figure 7).

Only three meta-analytical questions involved divorce, verifying the association between this behaviour with breeding failure before and/or after its occurrence (Dubois & Cézilly, 2002; Culina *et al.*, 2015; Culina & Brouwer, 2022). Other questions in this category explored the relationship between EPCs or EPP and certain traits, such as age (Cleasby & Nakagawa, 2012), ornaments or sexual signals (Table S8), parental care (Arnqvist & Kirkpatrick, 2005; Albrecht, Kreisinger & Piálek, 2006), pair relatedness (Arct, Drobniak & Cichoń, 2015; Hsu *et al.*, 2015), or a mix of these traits (Møller & Ninni, 1998; Akçay &

Roughgarden, 2007). In addition, a couple of these studies also tested whether offspring fitness is associated with its genetic origin (intra- vs extra-pair; Arnqvist & Kirkpatrick, 2005; Akçay & Roughgarden, 2007).

(9) Sexual conflict and estimates of sexual selection

Here, we briefly review the 14 meta-analytical questions (each from a different study) that focused on the two remaining topics related to sexual selection: sexual selection estimates (see Fitze & le Galliard, 2011; Henshaw, Kahn & Fritzsche, 2016; Anthes *et al.*, 2017) and interlocus sexual conflict (Parker, 1979; Chapman *et al.*, 2003) (Figure 7).

Two meta-analytical studies explored sexual selection on traits using standardised selection gradients (β: regression between standardised trait values and relative fitness, Lande & Arnold, 1983). As a fitness proxy, Hoekstra *et al.* (2001) used mating success, whilst Dougherty & Shuker (2016) used both mating and insemination success. Other estimates of sexual selection, such as Bateman's gradient (β_{ss}: average reproductive success gains from each additional mating; Bateman, 1948) and opportunity for sexual selection (I_s *or* I_{mates}: variance in relative mating success; Wade, 1979; Shuster & Wade, 2003), were much more common in our dataset (Table S8). Macedo-Rego *et al.* (2020a, 2020b) also used the Jones' index (s'_{max}; Jones, 2009), albeit Moura & Peixoto (2013) made their own estimate (I_{dif}: I_s if mating were random minus observed I_s). Aside from verifying the mean estimates of sexual selection found in the literature, several meta-analyses investigated whether these estimates were associated with other variables, like availability of reproductive sites (Alissa, 2018), monopolisation of mates (Macedo-Rego *et al.*, 2020b), operational sex ratio (Moura & Peixoto, 2013; Janicke & Morrow, 2018), sexual size dimorphism (Janicke & Fromonteil, 2021), and species richness (Janicke *et al.*, 2018). Yet, estimates of sexual selection present several constraints regarding how they are computed, which was the main subject of some meta-analyses (e.g. how mating success is measured and whether zero mating success is included; Anthes *et al.*, 2017; Macedo-Rego *et al.*, 2020a). Note that these estimates of sexual selection do not actually take into consideration effects of mate quality (see Fitzpatrick, 2015).

At last, we found two meta-analytical studies with unique perspectives in the literature. First, Cally *et al.* (2019) assessed fitness consequences on a population level from experiments that enforced monogamy or manipulated adult sex ratio, essentially modulating sexual selection. Second, Gómez-Llano *et al.* (2023) evaluated the costs imposed by one sex on the fitness of the other sex through direct (e.g. traumatic insemination) and/or indirect (e.g. harassment) harm, the only study on sexual conflict in our dataset.

(f) Focal sex

Sex roles conformist (i.e. focus only on males, except for questions on mate choice) and neutral approaches dominate meta-analytical studies related to sexual selection (Figure 9). A single study exclusively focused on hermaphrodite animals (Graham *et al.*, 2015), and 14 studies did not clarify the sex of individuals they focused on for any of their questions. Non-conformist approaches only preponderate over others on questions regarding remating and eagerness to copulate, as studies on this topic essentially tested the benefits and costs of polyandry (see section III.2.e.5). Conversely, questions on mating patterns are more sex-neutral than others, but this might simply reflect their inherent approach using data from (heterosexual) social pairs or couples in copula. However, we emphasise that questions from other topics that are answered with sex-neutral data might still show a skewed ratio of males and females in their dataset. For example, White (2020) evaluated whether structural colours are associated with individual quality in both sexes, but 146 effect sizes were from males and only 29 were from females. This sex imbalance is quite common in other (not so) sex-neutral meta-analyses from our systematic map, confirming that sex bias is a reality in the field of sexual selection (see also Tang-Martinez, 2016; Pollo & Kasumovic, 2022).

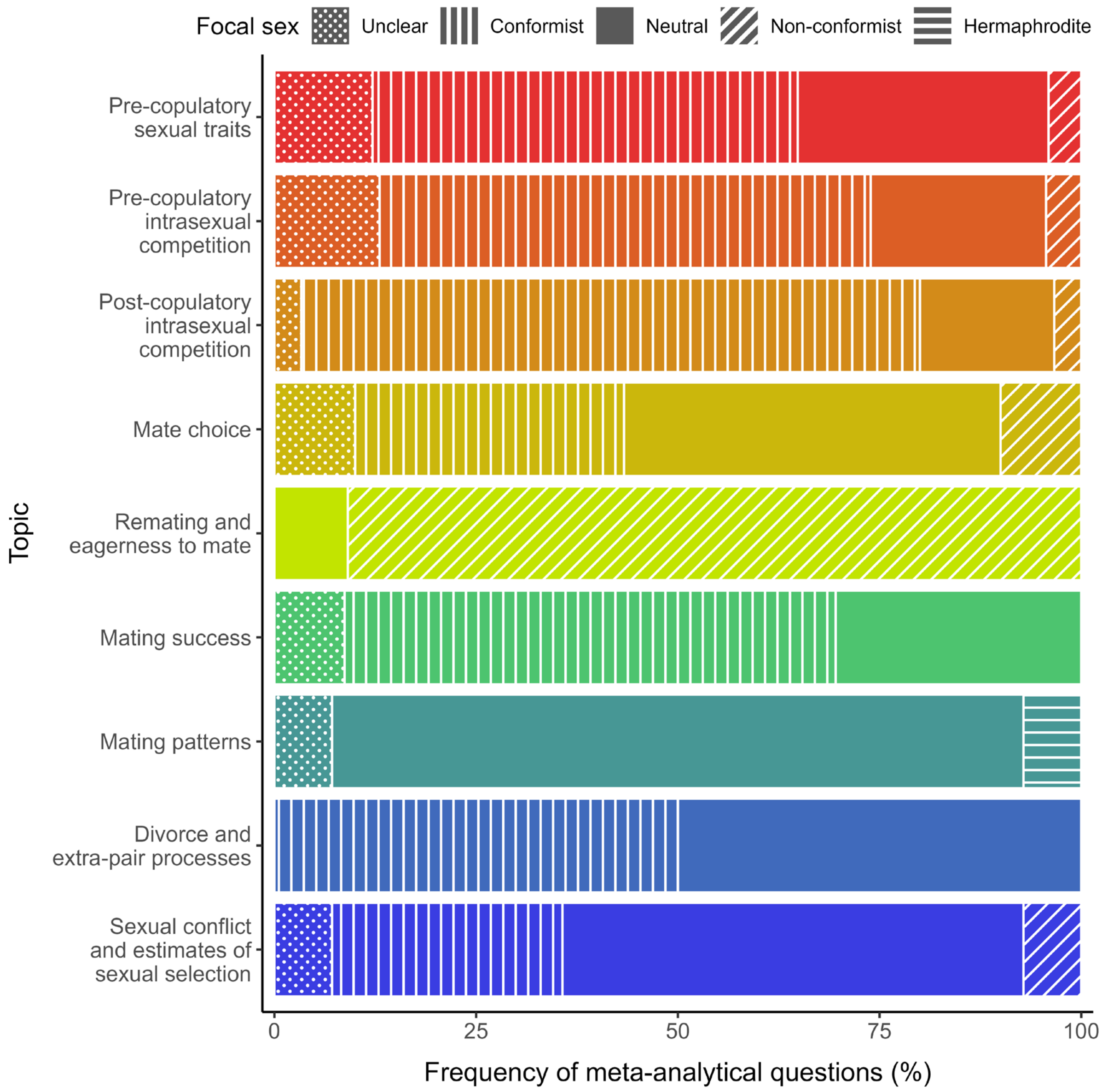

Figure 9. Focus of meta-analytical questions in relation to the sex of individuals used and the topic explored (see details in-text). Conformist refers to exclusive focus on males, and non-

conformist refers to exclusive focus on females (except for mate choice, in which this rationale is inverted). Neutral refers to both sexes being the focus of a meta-analysis.

The fact that the empirical and meta-analytical research literature investigates certain reproductive behaviours mostly in one sex potentially reflects and contributes to researchers' sex stereotypical perceptions of the animal kingdom (Pollo & Kasumovic, 2022; Ah-King, 2022a, 2022b). Darwin (1859, 1871) started this process: at first, he defined sexual selection as an evolutionary pressure acting exclusively on males, and frequently employed sexual stereotypes in his work. Although since then researchers have advanced our knowledge on both sexes, the need to reduce sex bias in the field of sexual selection remains dire (Pollo & Kasumovic, 2022; Ah-King, 2022b). In particular, researchers have emphasised the importance of not neglecting females in the study of sexual selection and related topics (e.g. Gowaty, 1997; Hare & Simmons, 2019; Rosenthal & Ryan, 2022). For instance, even though post-copulatory processes may depend on females as much as on males, female genitalia and reproductive organs have been largely overlooked, highlighted by recent discoveries and definitions (e.g. Folwell *et al.*, 2022; Keeffe & Brennan, 2023; see also Ah-King, Barron & Herberstein, 2014). Furthermore, only two meta-analytical studies from our dataset presented questions exploring the interaction between female and male traits in this context: Joly & Schiffer (2010) evaluated whether (female) receptacle length is associated with sperm length, while Myers *et al.* (2020) assessed whether presence of ovarian fluid is associated with sperm motility. However, we cannot rule out that some meta-analyses were sex roles conformist simply because data for one sex were virtually inexistent (e.g. female alternative mating tactics are rarely reported, probably unnoticed; Svensson *et al.*, 2009; Neff & Svensson, 2013). By overlooking females (and males in certain topics, like mate choice), we cannot truly attest the validity of long-standing tropes in the field of sexual selection (e.g. "competitive males, choosy females"). That is, such stereotypes will remain assumptions unless we investigate males and females equally. Thus, we urge researchers (especially empiricists) to consider their role in contributing to the construction of a truly sex-neutral literature in the field of sexual selection (see also Ahnesjö *et al.*, 2020).

(3) Conceptual challenges and recommendations

(a) Danger of biases

Throughout our manuscript, we identified several biases related to the content of meta-analyses on topics related to sexual selection (e.g. on specific questions, taxonomic groups, focal sex, etc). However, this might simply reflect biases that already occur in the primary literature on sexual selection. For instance, although researchers might be interested in meta-analytical questions that can encompass all animals, data available are highly concentrated in certain animal groups (e.g. birds; see section III.2.a). Thus, it might be fruitless to expect that researchers interested in meta-analyses can solve these biases alone if the raw material (primary evidence) remains unchanged. In fact, proper meta-analyses are also systematic reviews, highlighting gaps in the primary literature and therefore serving as indicators of the extent of our empirical knowledge.

One source of generalised biases in the literature may lie in the current publishing system, which shows an obsession with "novelty" (Cohen, 2017; Brembs, 2019; Ottaviani *et al.*, 2023). Paradoxically, novelty is rarely defined by journals that request it, but possibly refers to new and impactful discoveries, albeit this is highly subjective (Brembs, 2019). On one hand, this can encourage the production of meta-analyses because of their great power to test hypotheses (but see section III.5). Indeed, meta-analytical studies are often published in prestigious journals (e.g. Weaver *et al.*, 2018; Nolazco *et al.*, 2022). However, meta-analyses in ecology and evolution commonly detect high heterogeneity among effect sizes (Senior *et al.*, 2016a, see also section III.4.e) and often fail to find factors that can explain much of this heterogeneity, mainly because relevant data are scarce. This means that continuing to generate empirical data is almost always necessary, regardless of the subject. Yet, the pursuit of novelty only reduces the reward of further empirical research on a topic, especially with methods, organisms (even if not the same species or even genus), or results that resemble already published studies. For example, a study on mate choice with a spider species becomes less valuable to the publishing system the more studies on mate choice there are with other spiders (even though there are more than 40,000 species of spiders). This perspective makes empirical research harder to publish in top-tier journals, ultimately discouraging scientists from producing empirical data that would be extremely valuable to build a solid foundation of the theory. In a system that hampers research endeavours because of some similarity with previous work, replication becomes almost impossible despite being pivotal to science (Kelly, 2006; Nakagawa & Parker, 2015; Fraser *et al.*, 2020).

Limited research replication has many negative impacts on meta-analyses. Not only does it reduce the amount of empirical data available, but it also precludes updates of meta-analyses because updates are not considered “novel”. Yet, meta-analyses eventually need to be redone to incorporate new data and to improve their methods (including transparent reporting, see section III.4). Consequently, older meta-analyses would benefit the most from being updated. Moreover, the fact that numerous decisions in a research project can generate different outputs (Gelman & Loken, 2013) also applies to meta-analyses. For instance, some meta-analytical studies addressed almost identical questions but had their own particularities and sometimes reached distinct conclusions (e.g. Pollo *et al.*, 2022; Dougherty, 2023). This only emphasises that how research is conducted is as important, if not more, than how novel the question or methods are. Therefore, we deem innovation as pivotal to advancements in the field of sexual selection if it does not sacrifice further research of superficially explored topics.

What else do we lose by maintaining biases in the overall literature on sexual selection? It is hard to predict: if a specific animal or topic can provide revolutionary insights into sexual selection (or a particular aspect of it) but no incentives to study such unexplored animals or topics exist, their potential will remain unrealised. History shows that scientific milestones, such as the discovery of penicillin by Alexander Fleming, can come from unplanned or unexpected events (Bennet & Chung, 2001). The same history also shows that researchers often miss to recognise these important discoveries when they are made. Just like Fleming's work, Bateman's (1948) contributions took decades to gain recognition, eventually becoming a cornerstone of sexual selection theory (Hoquet 2020). In other words, researchers do not always seem to be the best clairvoyants or judges when evaluating the impact of basic science. So why should we keep all our eggs in certain baskets? Some might justify that knowledge gaps persist because of existent research constraints (e.g. post-copulatory choice and chemical signalling are difficult to examine). Nonetheless, we believe that it is precisely because some knowledge gaps require more effort to be filled that they require more incentives. Without proper encouragement, scientists are compelled to research more of the same, which represents a safer option for their careers but ultimately slows science advances.

We are aware that evaluating questions' importance in basic science can be particularly challenging because, by definition, they are rarely linked to direct financial or social gains and thus lack predictable and measurable outcomes. As a result, established researchers that occupy powerful positions (e.g. editors, reviewers, grant committees) end up dictating which topics and taxa deserve recognition. Although research proposals and manuscripts are theoretically judged by their arguments, how compelling these arguments are can depend on the reader. For instance, an editor of a behavioural ecology journal might be more likely to accept manuscripts focusing on birds than the ones on other taxa if the editor assumes that birds are more appealing to readers. This can create a feedback loop as readers of the journal (and the overall literature if this bias is common) are more often exposed to articles on birds, thus under the impression that birds are more valuable precisely because of their popularity. This hypothetical scenario might seem unlikely to happen if we naively think of researchers as unbiased machines, but evidence suggests that researchers can be as biased as other people in society. For example, both reviewers and editors judged research manuscripts differently depending on authors' gender and affiliation at an ecology journal (controlling for manuscript quality; Fox, Meyer & Aimé, 2023; Srivastava *et al*., 2024). How can we be sure that a similar situation is not occurring regarding topics, taxa, and other aspects of research projects? Unfortunately, this remains a rhetorical question as there are no data available to answer it.

Here, we argue that equal attention should be given to research aspects in the literature related to sexual selection (e.g. taxa, topic, focal sex), so the gaps diminish and hopefully disappear altogether. We urge researchers (especially those in powerful positions) to reflect about how their biases can influence their decisions and the advancement of the field. That is because highly influential researchers essentially determine the direction of research efforts in their fields, a power that only ends when they die (Azoulay, Fons-Rosen & Zivin, 2015). Moreover, to investigate whether biases are at play due to editorial decisions, we defend that journals and research societies need to compare projects that they reward (e.g. accepted for publication, given awards to) with those that they do not (as done by Fox, Meyer

& Aimé, 2023). Although this might be unfeasible for journals with wider scopes, most common outlets for research on sexual selection should easily be able to collect data on the taxa and general topics of research they receive for publication. Applying affirmative actions would then be required to correct detected biases (e.g. minimum quotas for unrepresented taxa and topics). In fact, such affirmative actions should already be in place given the wide evidence of biases in the literature (here and elsewhere). By not acting on these issues, academia remains analogous to the fashion industry, with only a handful of people deciding what is in vogue (literally).

(b) Danger of vague terms

Darwin (1859, 1871) founded the field of sexual selection using jargon: he extensively used the terms "primary sexual characters" and "secondary sexual characters" in his work (attributing their creation to the surgeon and anatomist John Hunter). These terms, mainly secondary sexual characters, served as the backbone for Darwin's arguments on the existence of sexual selection. Whilst primary sexual characters refer to traits necessary for reproduction (e.g. gonads and genitalia), secondary sexual characters were used by Darwin to refer to traits that would supposedly be linked to mate acquisition but not reproduction itself. Secondary sexual characters are usually classified as ornaments (mate attraction) or weapons (intrasexual combat, see also McCullough *et al*., 2016), which also became ubiquitous terms in the literature related to sexual selection (e.g. Andersson, 1994; Andersson & Iwasa, 1996; Andersson & Simmons, 2006; Shuker, 2010; Hosken & House, 2011; Simmons, Lüpold & Fitzpatrick, 2017; Lindsay *et al*., 2019). Such popularity can also be seen for the term "sexual signal" (whose exact origin is unknown to us, but probably from the 1980s; e.g. Endler &

McLellan, 1988; Endler, 1992), which highlights the communicative function (i.e. role in inter-individual interactions) of secondary sexual traits.

Researchers interested in topics related to sexual selection commonly employ this jargon when describing their question and selection criteria in meta-analyses. However, the expressions mentioned above are vague and loosely used, potentially causing transparency issues. For instance, numerous traits are frequently classified as secondary sexual characteristics simply based on sexual dimorphism, without a proper examination of its role in mate acquisition or reproductive success. This practice creates problematic cases, such as body size, which is explicitly mentioned as a secondary sexual trait by some (e.g. Simmons *et al.*, 2017). Although evidence shows that males in many species benefit from larger bodies in male-male contests, leading to sexual selection on this trait and sometimes male-biassed size dimorphism (Andersson, 1994; but see Tombak, Hex & Rubenstein, 2024), this pattern is simply assumed at times. For example, Moore & Wilson (2002) relied exclusively on sexual size dimorphism as a proxy for sexual selection without the evidence that body size was truly relevant to reproduction in all species investigated. The precarity of this assumption becomes evident when several cases of sexual size dimorphism occur due to other types of selection on body size, such as fecundity selection resulting in females larger than males in many invertebrates (but see Pincheira-Donoso & Hunt, 2017). Furthermore, if secondary sexual characteristics are synonymous with sexually selected traits (see Wiens & Tuschhoff, 2020), then this term could also encompass primary sexual traits, which are often under sexual selection (e.g. genitalia can play a role in post-copulatory competition; Andersson & Simmons, 2006). Similarly, traits related to gametes (e.g. sperm velocity) appear to be in a conceptual limbo, as they are rarely associated with this lingo despite also being determinant for post-copulatory processes (but see Rico-Guevara & Hurme, 2019).

Mentioning sexual ornaments also requires clarification, as this expression simply alludes to shiny, elaborate, or extravagant traits used to attract mates. The colloquial meaning of the word “ornament” predates its scientific (sexual) meaning, and this is not a coincidence: we tend to be fascinated by what catches our eyes, highlighting that our own sensory bias might be unreliable to describe all traits and patterns in nature. Thus, at least theoretically, other kinds of traits (e.g. chemical, tactile, electric; Kramer, 1990; Johansson & Jones, 2007) can also be classified as ornaments despite being inconspicuous to us. Although we cannot escape our human condition when observing nature (see Kokko, 2017), it is crucial to acknowledge our biases, especially in meta-analyses that claim to explore general patterns related to sexual ornaments (section III.2.e.1). This also applies for other terms, such as weapons and sexual signalling, which tend to be used for morphological structures and acoustic displays, respectively. Moreover, sexual ornaments and sexual signals seem to be overlapping concepts, although the latter might also encompass signals used during agonistic encounters (e.g. threat signals). Overall, the many inconsistencies in the use of these expressions reveal that their careless application can be misleading.

Ultimately, the words researchers choose to describe their questions are pivotal because they define its scope and the required degree of detailing what exactly is being studied. The specific expressions linked to sexual selection we mentioned in this section tend to be quite abstract and thus represent a wider scope than specific terms that depict direct measurements (e.g. sexual signal vs. song frequency, respectively; Figure 10). The larger the scope of a question, the more likely the diversity of measurements included in a meta-analytical study will be (e.g. more distinct traits, methods, taxa), increasing the apparent generality of the results at the cost of its interpretability (Figure 10; Spake *et al.*, 2022). Many meta-analyses in ecology and evolution have a wide scope, which possibly explains the common pattern of high heterogeneity they detect (Senior *et al.*, 2016a). Greater heterogeneity means that a global effect size has less reliability and that moderators are decisive in understanding patterns (Spake *et al.*, 2022). In other words, the motto invoked by biologists "it depends" intensifies with heterogeneity. Yet, meta-analyses with wide-scope questions receive more attention and usually get published in prestigious journals precisely because they claim to settle theoretical conundrums with a single, concise estimate. Such a practice means that the meta-analyses that carry the most responsibility to untangle complex patterns are commonly the ones that highlight superficial results while downplaying their limitations. For instance, García-Roa *et al.* (2020) claimed to examine the effect of temperature on sexual selection, but details of their dataset could only be found in their supplementary material (very little information in-text). A closer inspection on their data reveals that most effect sizes for females were based on fecundity, which is far from being strictly related to sexual selection, casting doubt on the general validity of García-Roa *et al.* (2020)'s claims. Many other meta-analyses in our systematic map show a similar problem, asking wide scope questions with unclear sexual traits or sexual selection proxies (e.g. Møller & Alatalo, 1999; Møller, Christe & Lux, 1999; Weir *et al.*, 2011; Cally *et al.*, 2019; Hasik & Siepielski, 2022).

As we showed, the specific expressions linked to sexual selection refer to diverse traits and patterns found in nature, being inherently loosely defined. Researchers thus need to be careful when using these terms in meta-analyses, clarifying what they truly encompass so readers can understand their study's focus and limitations. Clarification can be done by choosing the appropriate words that describe their research questions and goals (Figure 10) as well as by showing detailed information on the data searched and utilised in the manuscript, rather than just in the supplementary material. We also emphasise that, as the scope of a question (and consequently of the study) gets wider, moderators and meta-regressions become increasingly necessary to avoid false generalisations (Nakagawa *et al.*, 2017; Spake *et al.*, 2022; see section III.5).

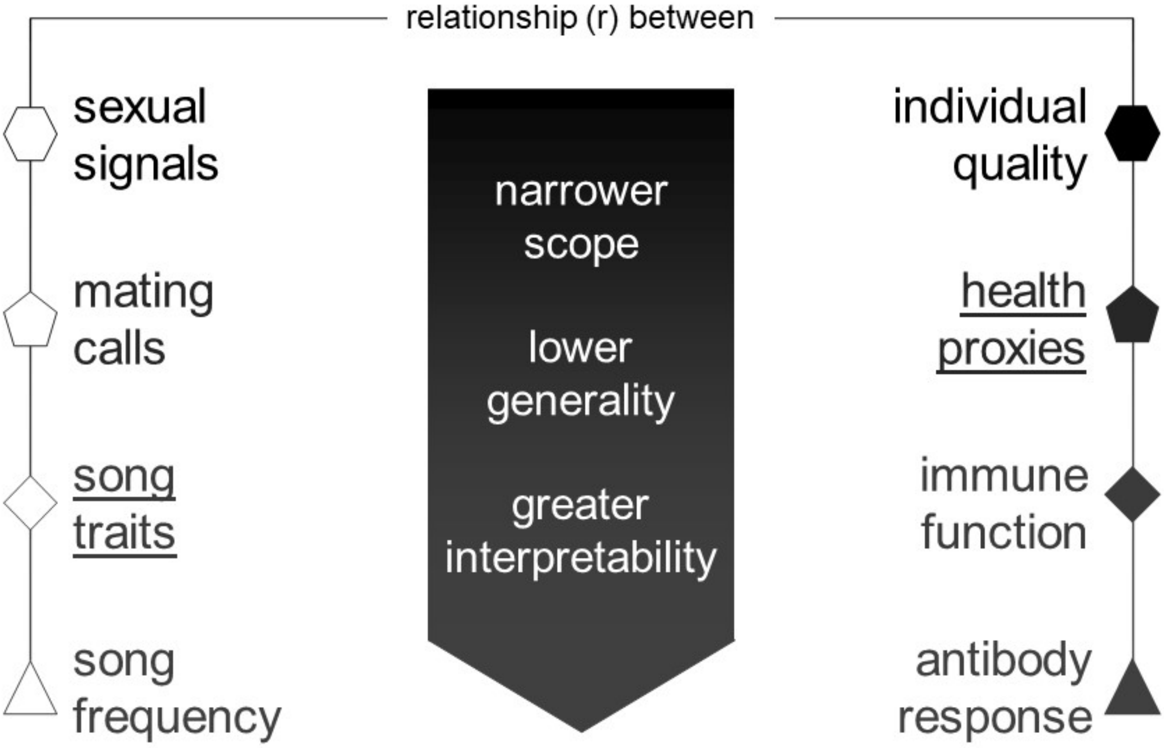

Figure 10. The specific words used in a question (e.g. whether two variables are related, denoted as "r") are associated with their scope, generality, and interpretability. Shapes with fewer vertices represent terms with narrower scope, less general, and more interpretable. Terms underlined highlight our suggestion for an overarching question in Garamszegi (2005): "is song expression associated with health proxies?" (see section III.5).

(4) Reporting appraisal of traditional meta-analyses

Almost 80% (119 out of 152) of the studies included in our systematic map (i.e. broad sense meta-analyses, see section II.2) were classified as traditional meta-analyses (i.e. used traditional effect sizes and properly modelled heterogeneity using additive weighting rather than multiplicative weighting; see Nakagawa *et al.* (2023a). The remaining studies (33) used other comparative methods, from simple linear regressions on raw data (e.g. Bailey & Hammond, 2003) to more sophisticated statistical approaches (e.g. Wang *et al.*, 2019 used formal effect sizes and mixed effects models with multiplicative weights where heterogeneity cannot be easily obtained). In this section, we evaluate methodological details only from traditional meta-analyses, as other comparative studies commonly do not adhere to classic meta-analytical standards. Figures 11 and 12 summarise the results of our appraisal, which are comparable to other similar studies (e.g. Philibert, Loyce & Makowski, 2012; O'Leary *et al.*, 2016; O'Dea *et al.*, 2021; Nakagawa *et al.*, 2023b; Yang *et al.*, 2023a).

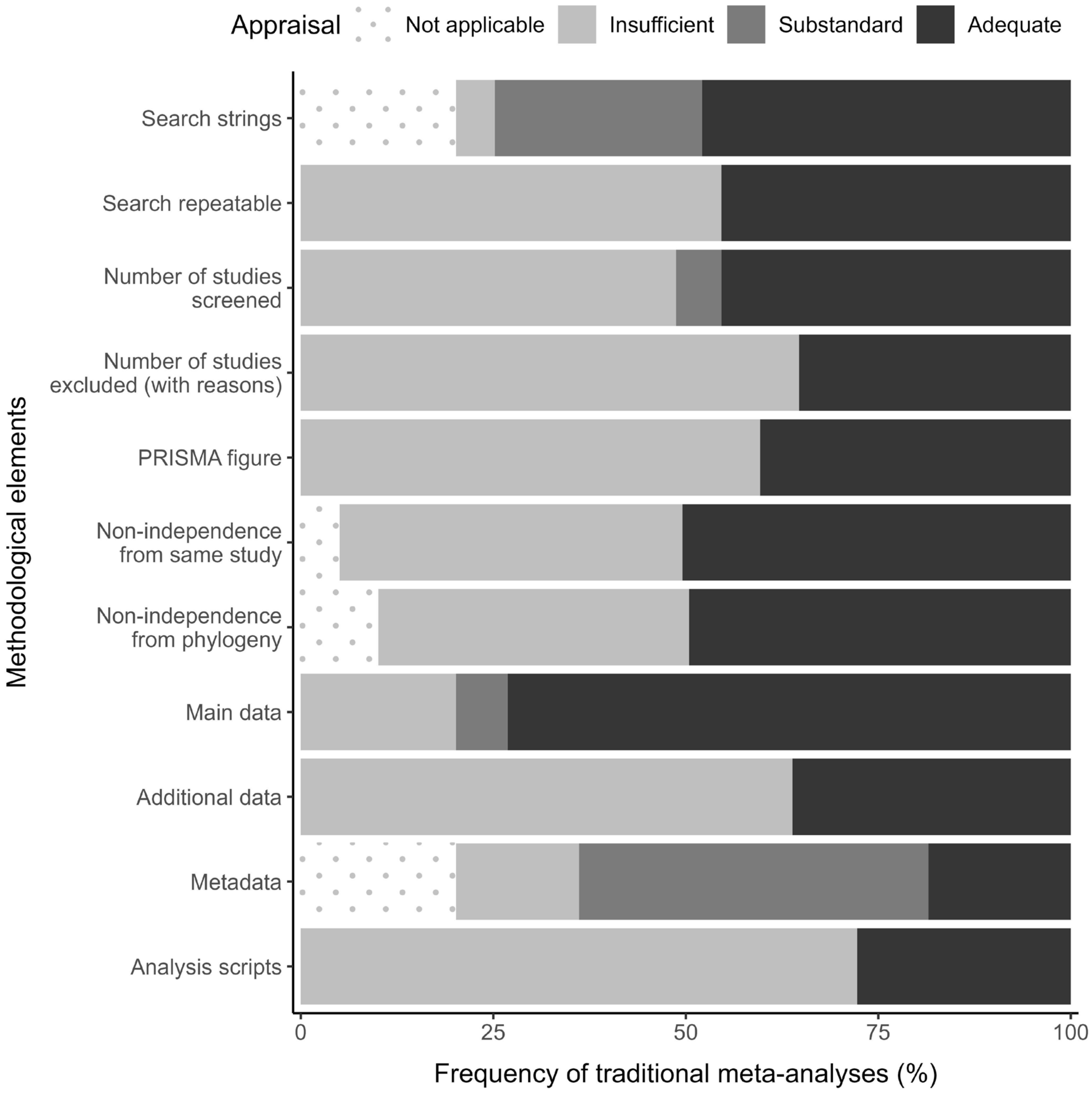

Figure 11. Appraisal of traditional meta-analyses on topics associated with sexual selection regarding several methodological elements. Elements poorly provided or absent were considered “insufficient”. “Substandard” appraisal was given to elements that were provided but with caveats, while “adequate” appraisal was given to elements competently provided. Certain elements were not applicable to be judged depending on the meta-analytical study (see details on section III.4).

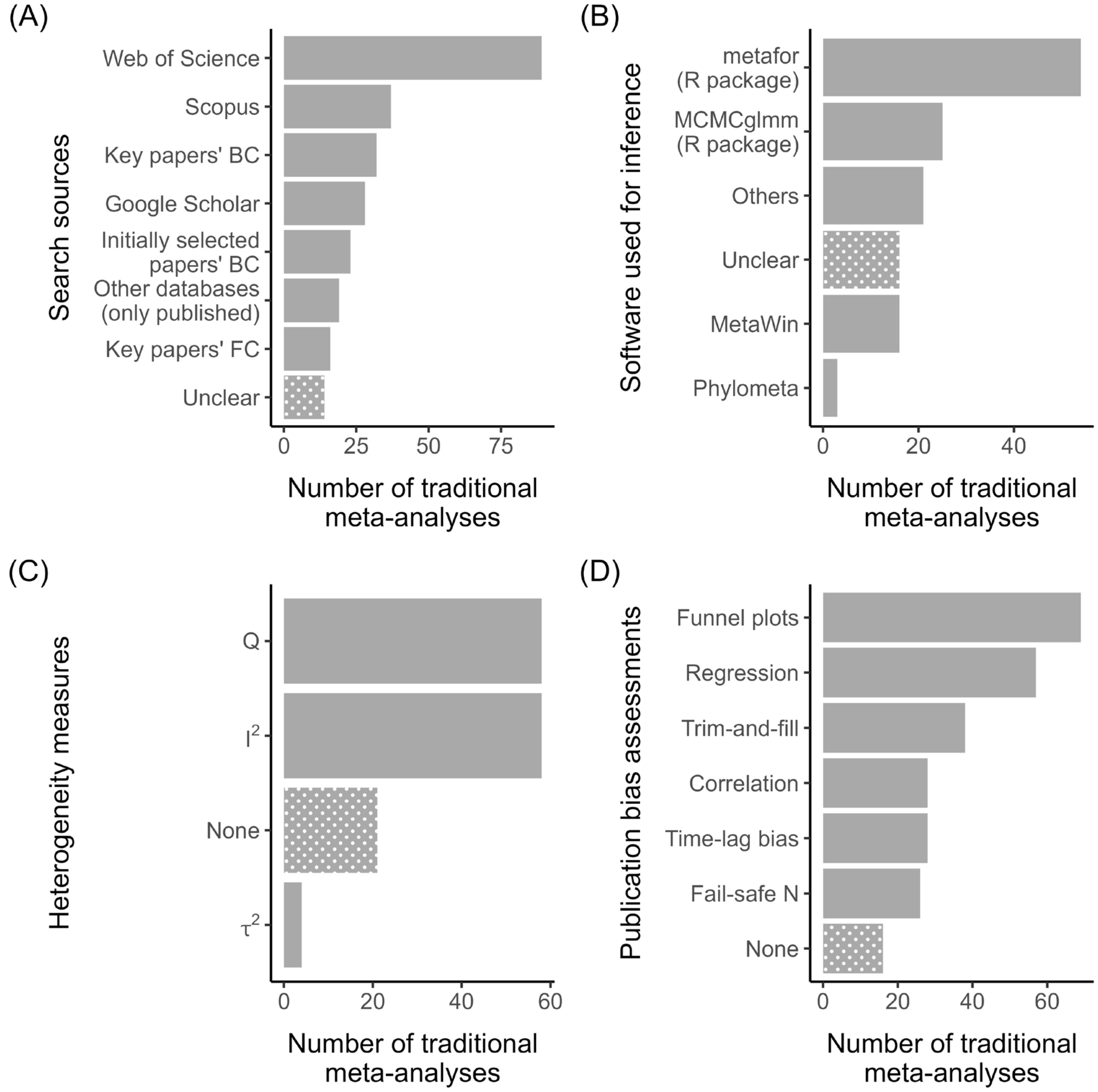

Figure 12. Details of methodological elements used by traditional meta-analyses on topics associated with sexual selection. Note that each meta-analysis could utilise multiple search sources (A), software (B), heterogeneity measures (C), and publication bias assessment tools (D), so the sum of values reported in each plot exceeds the number of traditional meta-analyses in our dataset (119). In the left top plot (A), 'BC' refers to backward citations and 'FC' to forward citations.

(a) Searches

Meta-analyses should describe their search methods in detail to enable repeatability of the search process (i.e. retrieval of the same set of empirical studies). This first involves describing the exact sources used to conduct searches reported in 88% of the traditional meta-analyses. In these meta-analyses, the most popular search sources were databases (e.g. Web of Science, Scopus), followed by backward citations (i.e. reference lists) from relevant key studies or initially selected studies (Figure 12A). These sources usually do not capture grey literature (i.e. unpublished studies). Sources that can capture grey literature (e.g. Google Scholar, BASE, etc) were used in less than a third (38 out of 119) of the meta-analyses. Yet, the number of meta-analytical studies that used grey literature is likely to be lower (searches may return no relevant results), highlighting a vexing aspect of meta-analyses in the field of sexual selection. This is because grey literature is commonly associated with the file drawer problem (i.e. studies with non-significant results are more likely to remain unpublished) and, therefore, is essential to reduce publication bias (Haddaway & Bayliss, 2015). In addition, every meta-analytical study should use multiple search sources to be comprehensive: we found that 68% of traditional meta-analyses used at least two search sources.

Next, repeatable meta-analytical studies also need to provide the exact queries used in database searches (McGowan *et al.*, 2016). However, less than half (48%) of all traditional meta-analyses complied with this guideline. Another 27% simply provided a list of individual keywords used in database searches without boolean operators connecting them, which represents a substandard provision of information as it hinders search reproducibility (Figure 11). We note that the remaining meta-analyses from our dataset provided no search strings, with the distinction that the ones classified as “not applicable” include cases whose search sources were unclear or did not use online databases (possibly forgoing the need for search queries), whilst the ones classified as "insufficient" conducted database searches.

We further assessed the repeatability of searches conducted in traditional meta-analyses, using the information we collected about search sources and queries (for which substandard string provision was not considered repeatable) coupled with other details. For instance, repeatable searches had to both specify when they were conducted (at least month and year) and their sources had to be accessible in 2023 (some older databases were no longer available). We found that traditional meta-analyses' searches from our dataset were repeatable in approximately 45% of the cases (Figure 11).

(b) Screening process

Meta-analytical studies need to be transparent with their screening decisions, explicitly reporting the number of studies screened and the number of studies excluded at the full-text screening stage with justifications that clarify each of these exclusions. Thus, we first verified whether traditional meta-analyses provided the number of studies screened in at least two screening phases (i.e. initial and full-text). We considered the screening information provided to be "insufficient" when the number of studies screened were absent, as "substandard" when this number was reported for only one phase or when it was not exact (e.g. Hasik & Siepielski, 2022), and as "adequate" when screening information was detailed for both initial and full-text phases. This resulted in 49%, 6%, and 45% of traditional meta-analyses from our systematic map showing insufficient, substandard, and adequate information on the number of studies screened, respectively (Figure 11).

We then verified details on screening decisions, in which we deemed as insufficient information when studies provided no information, only information for their initial screening phase (e.g. Nolazco *et al.*, 2022), or a list of exclusion reasons with the total number of excluded studies (instead of exclusion reason for each study, e.g. Weaver *et al.*, 2018). This culminated in only 35% of traditional meta-analyses properly describing the justification for their full-text excluded studies (Figure 11).

Both the number of studies screened and excluded (with justifications) should ideally be presented in a PRISMA-like diagram, which summarises both the search and screening processes (O'Dea *et al.*, 2021). A few studies presented figures that lacked too many necessary diagram elements, so we considered them insufficient (e.g. Harts, Booksmythe & Jennions, 2016; Hasik & Siepielski, 2022). We found that only 40% of the traditional meta-analyses from our dataset showed adequate PRISMA-like diagrams (Figure 11).

(c) Software and data non-independence

Non-independence among effect sizes often occurs in meta-analyses, which can lead to false conclusions if not properly addressed (Noble *et al.*, 2017; Cinar, Nakagawa & Viechtbauer, 2022). We specifically examined whether traditional meta-analyses from our dataset dealt with non-independence from shared study identities (i.e. when at least two effect sizes are extracted from the same study) and from phylogenetic relatedness. We found that approximately half of the meta-analytical studies dealt with at least one of these non-independence sources (Figure 11), usually through random factors in meta-analytical models. We emphasise that non-independence might be entirely absent (i.e. not applicable; Figure 11) from meta-analyses whose effect sizes are all extracted from different studies (i.e. independent) or when they investigate only a single species (see section III.2.a). Related to this, most meta-analyses were conducted using the R packages *metafor* (Viechtbauer, 2010) and/or *MCMCglmm* (Hadfield, 2010) (Figure 12B). These packages are the most appropriate meta-analytical tools as they can incorporate phylogeny and other types of non-independence.

(d) Analytical reproducibility and transparency

We evaluated whether meta-analyses transparently provided the main components needed for analytical reproducibility: sharing of the main data, metadata, additional data, software information, and analysis scripts. Lack of data transparency is a major obstacle for reproducibility (Wilkinson *et al.*, 2016; Munafò *et al.*, 2017). First, meta-analyses need to provide data with effect size values and all other variables used in their analyses (e.g. moderators). We refer to these datasets as the main data, as studies can also provide additional data (e.g. raw measurements or location from which they were extracted in empirical studies). We found that 73% and 7% of traditional meta-analyses provided all or some (i.e. substandard) of their main data, respectively (Figure 11). These findings are a little more optimistic than those found by a survey of the primary literature in ecology and evolution (Roche *et al.*, 2015; Kambouris *et al.*, 2024). However, we note that many datasets were simply provided in a form of tables in-text (rather than separate data files), which is considered as a suboptimal practice. In addition, data were supposedly provided but could not be accessed in some cases (e.g. due to broken links; Guindre-Parker & Love, 2014; Dougherty, 2023), emphasising that authors must ensure that any resources mentioned in their studies are truly available to readers. Despite main data being shared in most meta-analytical studies, only 36% of meta-analyses evaluated provided additional relevant data (Figure 11), highlighting another obstacle for reproducibility.

To enhance reproducibility, data should ideally be provided with a separate metadata file (i.e. information that fully describes all fields from the main dataset provided). Metadata were provided in only 18% of traditional meta-analyses (Figure 11). Nonetheless, another 45% of the studies showed easily understandable data (e.g. from the study context, no acronyms used) and, even though we considered these cases as substandard for lacking proper metadata (Figure 11), these resources were occasionally clear and informative (e.g. tables in Meunier *et al.*, 2011; Graham *et al.*, 2015). We also note that metadata were not applicable for traditional meta-analyses that did not provide any of their main data (ca. 20%).

At last, sharing analysis scripts is essential for others to reproduce meta-analytical findings (Piccolo & Frampton, 2016; Culina *et al.*, 2020). We found that only 28% of the studies evaluated in our appraisal appropriately shared their code (Figure 11). The remaining 72% either used point-and-click software (n = 27; e.g. MetaWin, Phylometa, etc; Figure 12B), did not mention the software used (n = 16; although some studies might have not used any, e.g. manual calculations), or simply provided no code despite using other software (n = 43). Our finding is similar to recent reports on code availability in ecology (Culina *et al.*, 2020; Kambouris *et al.*, 2024). The low code sharing can be a result of lack of incentives for authors to share their code (see Gomes *et al.*, 2022) or lack of the awareness of the importance of software in research.

(e) Heterogeneity and publication bias

Heterogeneity measures the amount of variation among effect sizes, thus being critical to understanding the generality of overall effect sizes shown in meta-analytical studies (Spake *et al.*, 2022; see section III.5). We found that 82% of traditional meta-analyses calculated at least one heterogeneity measure. Those that did most frequently used Q and/or I^2 (Figure 12C). We note that H^2 (Lynch, 1991) or Pagel's λ were commonly present in phylogenetic regressions, which we did not consider proper stand-alone heterogeneity measures for a meta-analysis.

Meta-analytical studies also must investigate publication bias in their included dataset, as this can drastically impact results' magnitude and sign errors (Yang *et al.*, 2023b). 87% of traditional meta-analyses from our dataset assessed publication bias in some way. Funnel plots were the most popular tool to address publication bias (Figure 12D), similar to Nakagawa *et al.* (2021)'s findings.

(f) Other elements

We verified the occurrence of several other important methodological elements in traditional meta-analyses, but rarely found them. For instance, only one study was pre-registered (e.g. Kim *et al.*, 2021) and none mentioned post-hoc hypotheses (although some mentioned post-hoc analyses; e.g. Winternitz *et al.*, 2017; Parker *et al.*, 2018; Kim *et al.*, 2021). In addition, only four traditional meta-analyses evaluated the quality of empirical data: Simons & Verhulst (2011) and Parker *et al.* (2018) examined empirical pseudoreplication, Kim *et al.* (2021) intended to verify the effect of blind data collection (but ironically found that no empirical studies collected data blindly), and Culina, Radersma & Sheldon (2015) evaluated the trustworthiness of empirical studies from which they extracted data. This near absence of quality assessment of primary studies has also been detected in ecological systematic reviews despite being imperative to reduce bias (Stanhope & Weinstein, 2022). However, the lack of a standard evaluation tool for risk-of-bias in ecology and evolution might be the culprit for this dismal situation. Also, we emphasise that here we only considered generic quality assessments (i.e. that are relevant for all types of studies), but that there are also more specific assessments (e.g. via experiment design; (Davies, Lewis & Dougherty, 2020; Pollo, Nakagawa & Kasumovic, 2022).

(5) Analytical challenges and recommendations

Several papers and books specifically targeted at ecology and evolutionary biologists provide helpful recommendations on how to conduct meta-analyses. Their focus ranges from initial procedures that are also part of systematic reviews (e.g. search and screening) to specific statistical methods (e.g. Nakagawa & Cuthill, 2007; Nakagawa & Santos, 2012; Koricheva *et al.*, 2013; Noble *et al.*, 2017; Foo *et al.*, 2021; O'Dea *et al.*, 2021; Nakagawa *et al.*, 2021; Spake *et al.*, 2022; Yang *et al.*, 2023b). Nonetheless, we noticed that many meta-analyses included in our systematic map conduct precocious subset analyses (i.e. practice of partitioning the extracted data and then fitting a separate meta-analytical model on each subset without a global model). This procedure often leads to a mismatch between the general question asked in the study and its respective statistical analysis. In this section, we use a fairly simple meta-analysis (Garamszegi, 2005) to illustrate our argument (see also Figure 10).

Garamszegi (2005) examined the relationship between distinct bird song traits and health proxies (e.g. parasite prevalence or immune function). Intuitively, one can assume that this study asks "is song expression associated with health proxies?". Yet, Garamszegi (2005) shattered the expectation of a single answer (e.g. through a global mean effect size) by presenting four separate mean effect sizes, each related to a different song trait (performance: song rate; complexity: repertoire size; duration: call length; and frequency). This exemplifies precocious subset analysis, and we argue that this approach generates two issues.

First, the reader is left without an answer to a general question (even if it is a vague one). Garamszegi (2005) only provides answers to separate, specific questions (e.g. does song frequency reflect health?; does song complexity reflect health?; etc). Second, subset analysis could increase error type I (i.e. rejecting a true null hypothesis) when compared with a unified, random-effects (multilevel) model (cf. Nakagawa & Santos, 2012; Nakagawa *et al.*, 2022). Third, effect sizes from groups analysed with different models cannot be statistically compared. Fourth, it limits the test of other moderators and their interactions. For example, Crean & Senior (2019) verified the effect of high-fat diets on model mammals regarding different sperm traits and several measurements of reproductive success, but each of these traits and measurements (17 in total) was analysed separately, meaning that the role of moderators (diet duration, specimen age, etc) could not be assessed across all effect sizes (only within each subset). Why analytical fragmentation has been employed so often is unclear, but we suspect that researchers' concern of being accused of making unfair comparisons through wider-scope models has increased the use of this approach. Alternatively, researchers may simply believe that each sub-question requires a separate meta-analytical model. Regardless of the reason, we believe it is crucial to discuss the benefits and disadvantages of each approach.

Analysing data separately may seem fair at first glance: meta-analyses are often criticised for clumping conceptually distinct data to make inferences (i.e. "mixing apples and oranges"; Arnqvist & Wooster, 1995; Noble *et al.*, 2022). Although meta-analyses in other fields are not exempt from this complaint, the diversity of methodologies, biological traits, mechanisms, and patterns across species and empirical studies makes meta-analyses in the field of ecology and evolution particularly prone to this criticism. However, researchers have little option other than categorising measurements to make comparisons. For example, although Garamszegi (2005) analysed song traits separately, each one of them still included different measurements (e.g. song frequency involved both lowest and highest frequency, as well as frequency range). Moreover, parasite prevalence and immune function were analysed together, revealing that this author deemed them analogous measurements. Therefore, subsetting the analysis did not avail Garamszegi (2005) to entirely escape from mixing apples and oranges, essentially because it is inevitable to do so to a certain extent (Rosenthal, 1991). In other words, researchers can rarely avoid a certain degree of abstraction in interpreting results of meta-analyses in ecology and evolution because of the inherent variability in this field.

We suggest to researchers to, foremost, carefully define a question using the PECO/PICO framework (Richardson *et al.*, 1995; Foo *et al.*, 2021) that encapsulates all subquestions (if possible). Although multiple specific questions can be asked in a single meta-analytical study, they often can be summarised into a more general one, as we have shown for Garamszegi (2005). This allows researchers to conduct one or few models with predictors (i.e. moderators) that can potentially explain the variation found, emphasising their effectiveness or lack thereof in doing so (Spake *et al.*, 2022), instead of fragmenting the data and analysis into multiple subsets from the start. These moderators fundamentally work as the specific questions that many authors ask when using subset analyses. A global model, however, becomes inadvisable when sub-questions are completely unrelated to one another so a more general question becomes infeasible (although this might be subjective) or when effect sizes calculated are distinct in nature (based on means vs. based on variances). This approach makes it even more critical that authors specify the direction of calculated effect sizes for each measurement before analysis, preferably based on grounded hypotheses (e.g. Dougherty, 2021a). Nonetheless, the direction of effect sizes can be modified ad-hoc if one of the subsets presents an opposite pattern, so that the global mean effect size can focus on magnitude rather than direction.

Researchers might still harbour suspicion over a global model approach in complex cases as, until now, we have only used a meta-analysis with relatively specific questions as an example (Garamszegi, 2005). Thus, consider Alissa (2018), who asked whether limitation in reproductive sites is associated with several measurements related to sexual selection (e.g. pre-copulatory intrasexual competition, sperm competition, selection on male traits, and opportunity for sexual selection). In this study, the author conducted several meta-analyses (i.e. subsets were independently analysed), probably because of wildly distinct measurements included in it. Although it would not be possible to combine opportunity for sexual selection with the other measurements because they are represented by distinct types of effect sizes in the study (lnCVR and Zr, respectively), all else could be grouped together. Grouping the effect sizes to estimate a single mean effect size would allow the author to compare the effect sizes for each measurement related to sexual selection. This global effect size would represent a more abstract and less interpretable estimate: whether reproductive site limitation is associated with various measurements related to sexual selection (see section III.3.b). However, the existence of a global mean effect size does not preclude researchers to focus on specific, narrow questions, which can be done with moderators and meta-regressions. Doing so would maintain the original conceptual structure in Alissa's (2018) manuscript while correcting its analysis.

Our recommendation to unify multiple, usually related questions to fit a single (or as few as possible) meta-analytical model does not mean to incentivize wider questions, but rather attempts to streamline analyses. In fact, focused meta-analyses (i.e. with narrow questions) can be more reliable because they are easy to interpret (Figure 10). Conversely, as previously mentioned (see section III.3.b), studies with wide questions that employ few or no meta-regressions might be of little use if they show highly heterogeneous estimates. Although the use of moderators might be constrained (e.g. due to too few data points), authors should at least justify these limitations and consider them to avoid misleading conclusions.

(6) Bibliometric analysis

The 152 meta-analyses included in our study were authored by 326 different authors affiliated to institutions from 31 countries (Figures 13 and 14). The median for the number of authors per study was three ($\bar{x}$ = 2.97, 95% CI = 2.71 to 3.24), while the median of the number of countries per study was two ($\bar{x}$ = 1.79, 95% CI = 1.63 to 1.95) (Figure 13). Intuitively, the number of different countries from authors' affiliations increased with the number of authors (Spearman's correlation: $r_s = 0.46$, $p < 0.001$; Table S11, Figure 13).

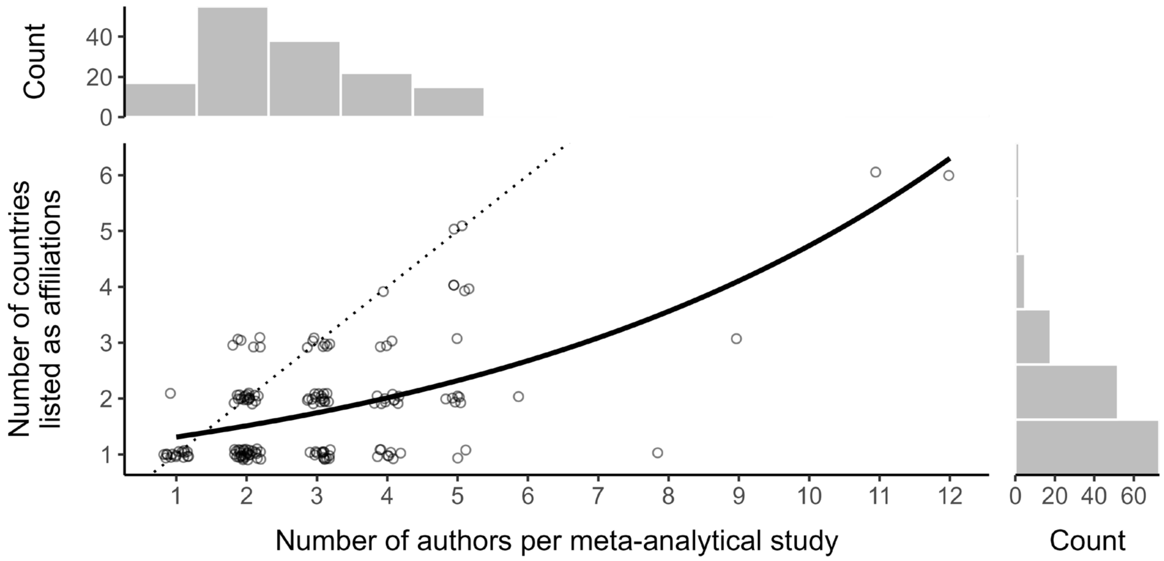

Figure 13. Relationship between number of authors for each meta-analytical study and number of countries listed as affiliations. The dotted line highlights a perfect relationship

between these two variables, while the solid line represents the best fit from a generalised linear model (Table S11). Histograms on top and on the right indicate the number of studies for each number of authors and countries listed as affiliations, respectively.

(a) Authors' affiliations

The United States of America (hereby USA) was the most prolific country in publishing meta-analyses on topics associated with sexual selection, with 42 meta-analyses being authored by at least one researcher affiliated to an institution located there (followed by Australia with 40 meta-analyses; Figure 14). We detected only a few developing countries (i.e. Global South) as affiliations in the evaluated meta-analyses. In fact, the only countries with more than a single study affiliated outside of Anglo-America, Europe, or Oceania, were Brazil and Mexico (Figure 14).

The first affiliation listed in each study, which is usually associated with the lead authorship, revealed a similar authorship pattern. The USA also led with the highest number (n = 26) of studies with one of its institutions as the first affiliation listed in studies, albeit the United Kingdom followed close behind with 24 first affiliations. The proportion of first affiliations to all affiliations seen per country can serve as a proxy of how dependent a country is on international collaborations (Figure 14). For example, despite seven meta-analytical studies being associated with an institution from Spain, only in one of them a Spanish institution was the first affiliation listed. In contrast, Belgian institutions were first listed as affiliations in all of five meta-analyses associated with Belgium. We emphasise, however, that this proportion tends to extreme values (i.e. none or all) with fewer studies associated with a country (Figure 14). Furthermore, we note that almost half of all meta-analyses evaluated (73 out of 152) were affiliated to a single country (Figure 14).

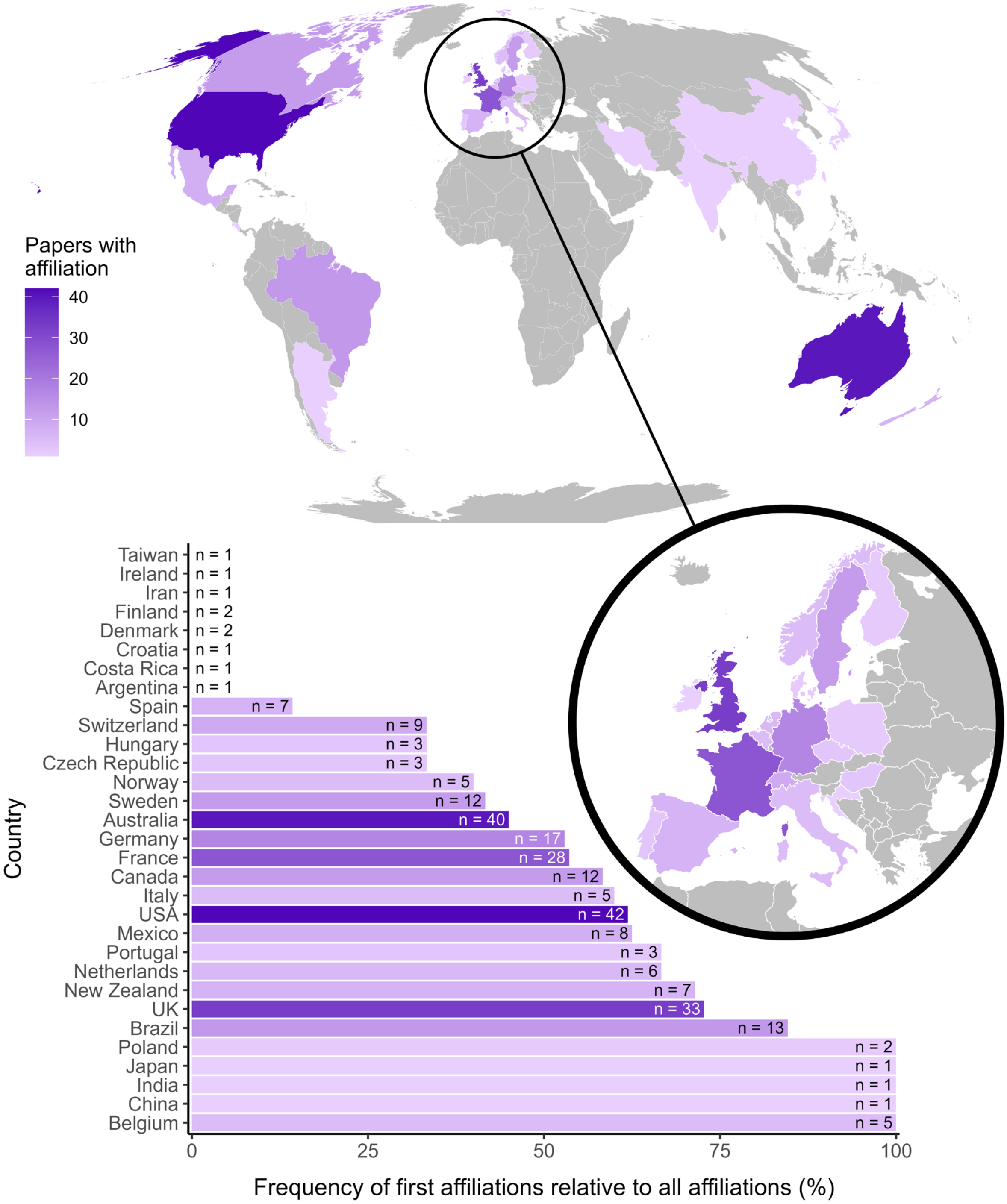

Figure 14. Affiliations reported in meta-analytical studies on topics associated with sexual selection. Colour intensity in maps (top and inset) illustrate the number of studies in which countries' institutions were recorded as authors' affiliations, greyed countries representing

zero. Bar plot (bottom) shows the percentage of affiliations that were reported first in studies (i.e. affiliation of first author) per country, with the total number of affiliations per country given inside each bar.

Shifting the focus to continents, we observed that approximately half (77 out of 152) of all first affiliations belong to Europe (Figures 14 and 15). Studies with first affiliations located in Europe were also more likely to be associated with institutions from multiple countries (and thus have international collaborations) compared to studies with other continents as first affiliation (Figure 15). However, most of these international collaborations were between countries in the same continent (Figure 15). For example, out of 48 meta-analyses that originated in Europe with multiple countries affiliated to them, 35 had at least one international collaboration with another European institution, while no author from another continent was involved in 25 of them.

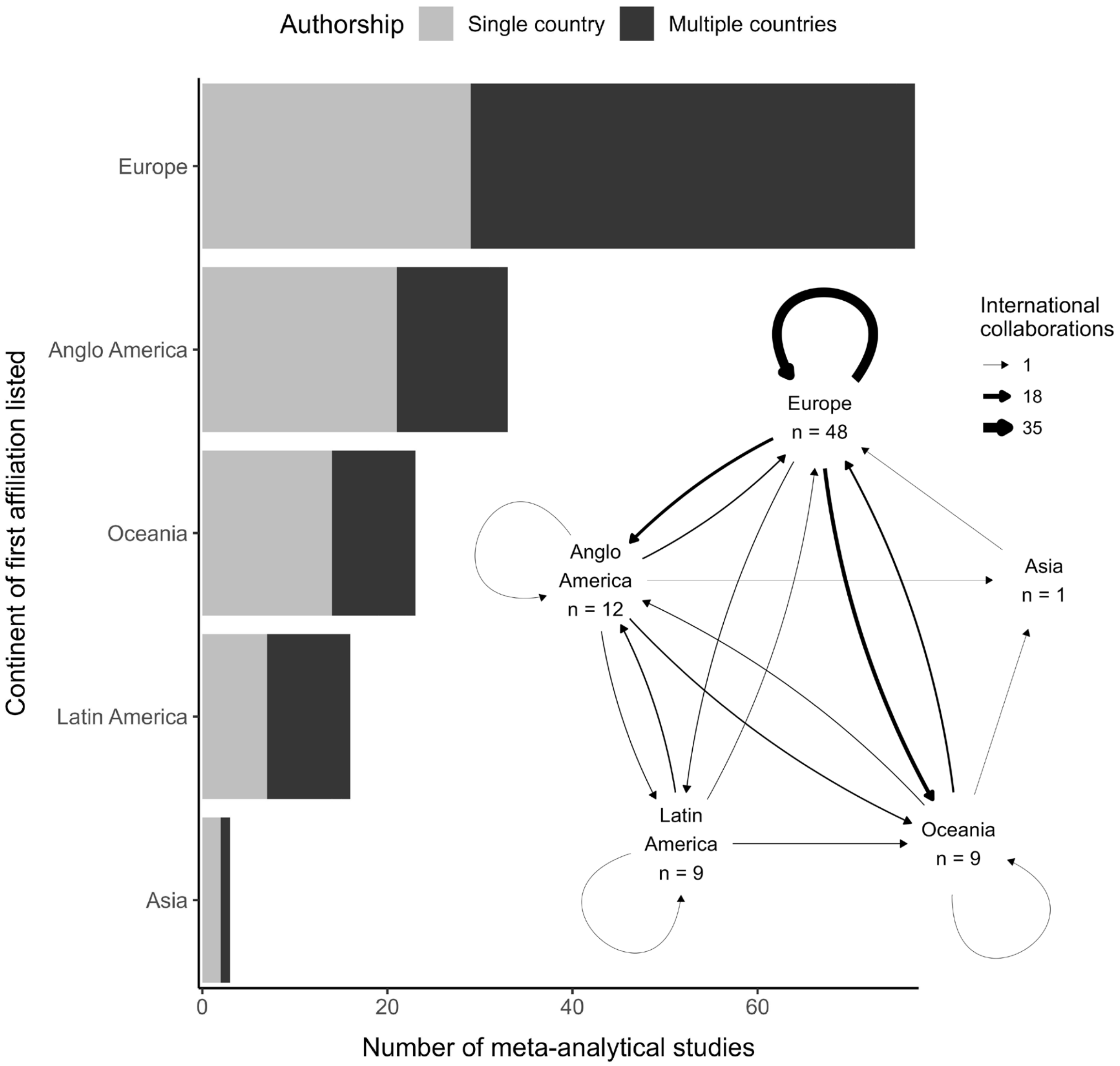

Figure 15. Collaborations on a continental level. The bar plot shows the number of meta-analytical studies per continent that listed affiliations from either one or multiple countries. The network shows the number of studies that contain affiliations from multiple countries (same as darker bars in the bar plot) per continent, with arrows representing international collaborations (from continent of the first affiliation to the continent of posterior affiliations).

(b) Authors' gender

We found gender bias in authors of meta-analyses on topics related to sexual selection: 37% of unique authors were classified as women (119 out of 321), opposed to 61% classified as men (195; gender could not be assigned to the remaining 2% of authors). This gender disparity increased when considering only first authors, as 68% of them (104 out of 152) were identified as men and 31% as women (47; 1% was unknown; Figure 16A). On average, women represented less than a third of the co-authors in multi-authored meta-analyses, indicating that men predominate in research projects even when they are led by women (Figure 16B).

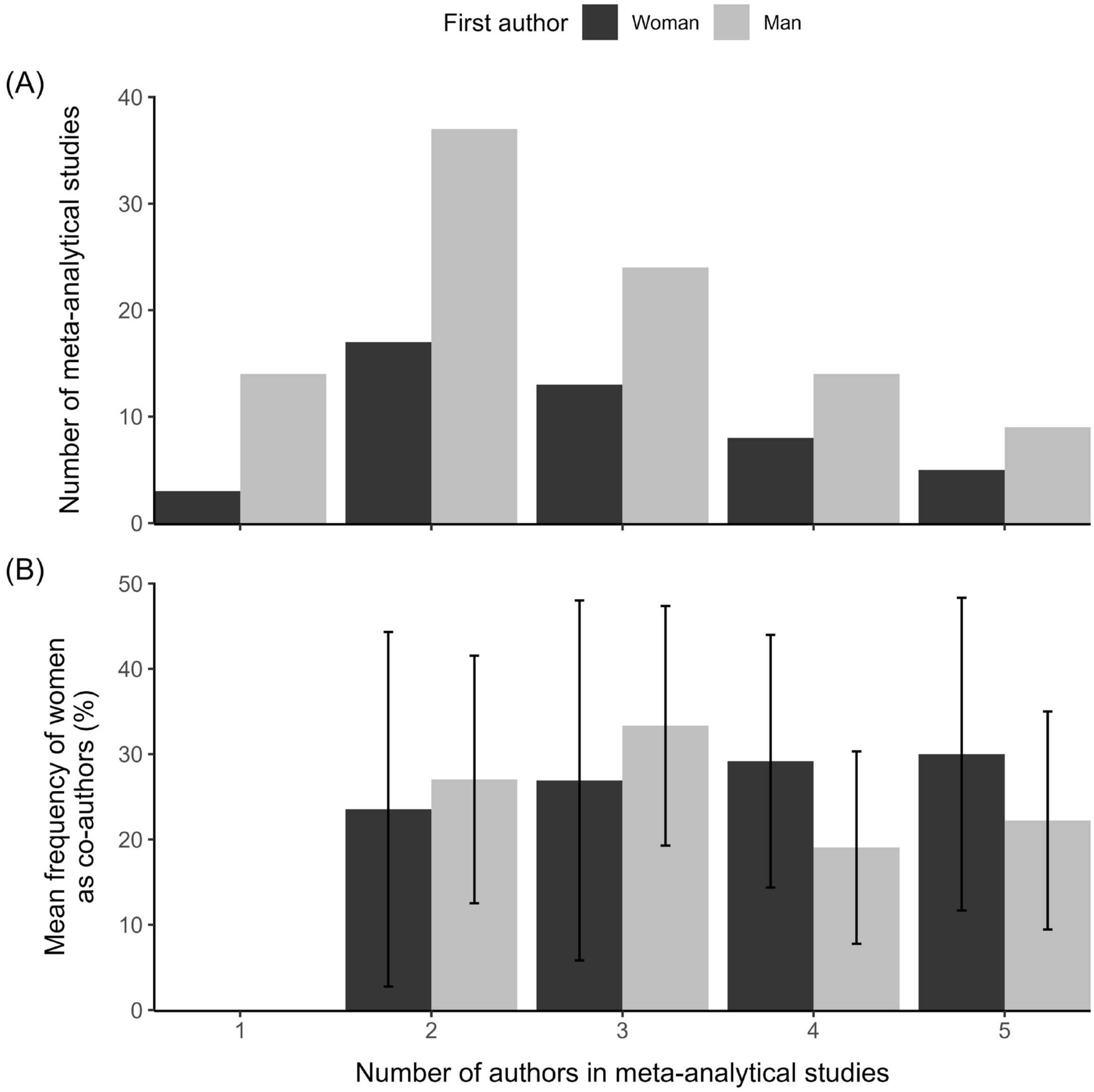

Figure 16. Number of studies (A) and mean frequency of women as co-authors (i.e. non-first authors; B) by gender of the first author and number of authors in meta-analytical studies on topics related to sexual selection. Four meta-analytical studies with more than five authors and another four that contained a name that could not be assigned to a binary gender are not shown. Whiskers in panel B represent the 95% confidence interval for the mean.

<u>(c) Authorship and literature gaps</u>

In an exploratory approach, we evaluated the relationship between several authorship aspects and four different gaps that we identified (taxonomic scope: section III.2.a, exclusive use of conformist or non-conformist sex: section III.2.f, and methodological transparency: section III.4; see also section II.4 for details on the analyses). We also controlled for publication year in our analyses, as authorship patterns could be related to temporal changes.

We found that the only authorship aspect related to meta-analyses' taxonomic scope was the proportion of women as authors: meta-analyses published by teams with proportionally more women were of narrower taxonomic scope (i.e. more likely to be on a specific species or animal group; Figure 17A; Tables S14 and S15). The gender of first authors was not related to meta-analyses' taxonomic scope, which suggests that women might be invited to participate more frequently in projects with specific taxa than in taxonomically unrestricted ones. In addition, we found that more recent meta-analyses were of wider taxonomic scope (i.e. more often taxonomically unrestricted; Figure 17B, Tables S14 and S15).

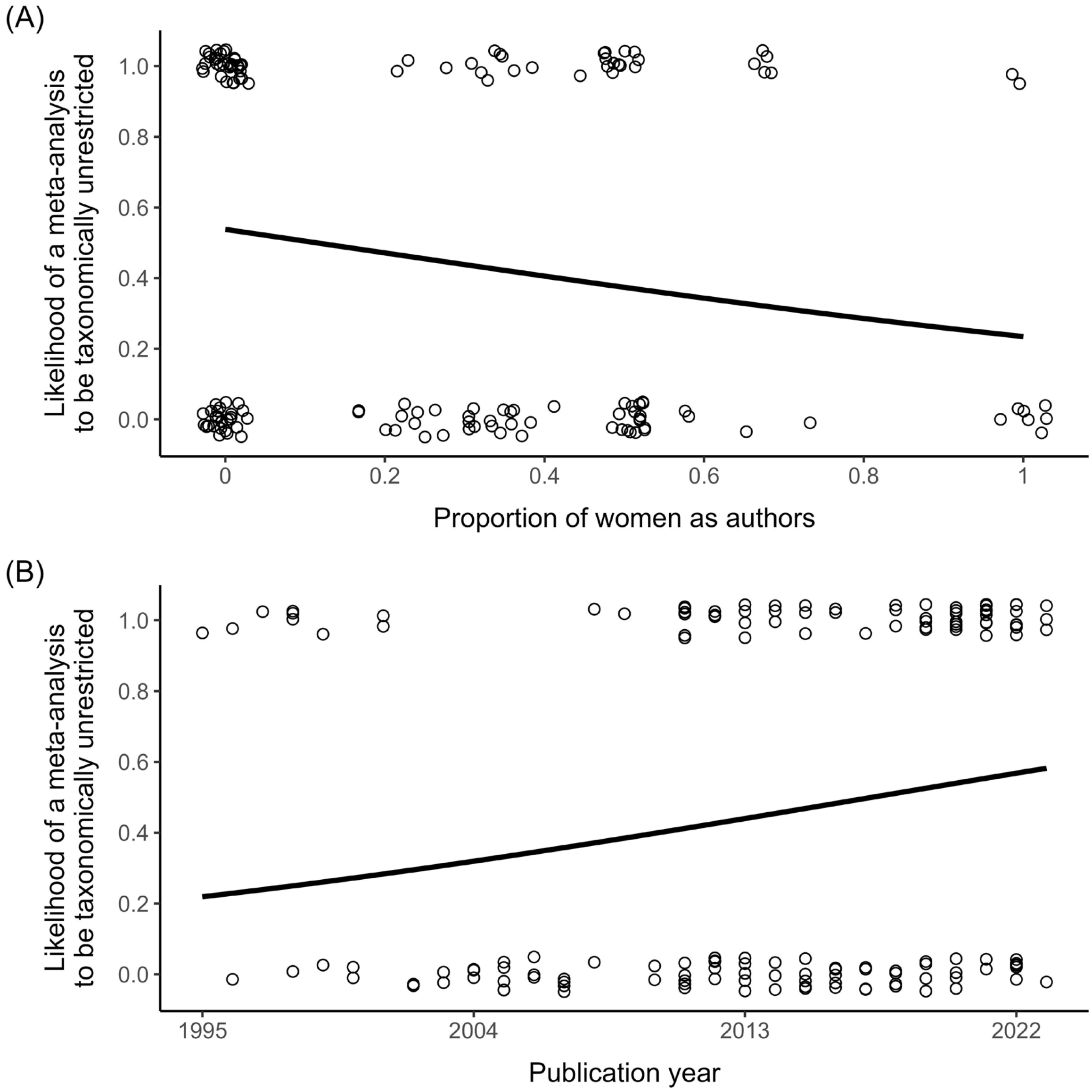

Figure 17. Relationship between taxonomic scope and the proportion of women as authors (A) or publication year (B) in meta-analyses on topics related to sexual selection. Solid lines represent the best fit from a generalised linear model (Table S15).

In contrast with taxonomic scope, we found no associations between authorship aspects and the exclusive use of the conformist sex (i.e. males for most topics, and females for mate choice) in meta-analyses on topics related to sexual selection (Tables S16 and S17).

Nonetheless, we identified that meta-analyses focused less on the conformist sex over time (Figure 18A, Tables S16 and S17).

We also identified that the likelihood of a meta-analysis to focus exclusively on the nonconformist sex (i.e. females for most topics, and males for mate choice) increased with the proportion of women as authors (Figure 18B, Tables S18 and S19). No other factor showed a relationship with exclusive use of the nonconformist sex, not even publication year.

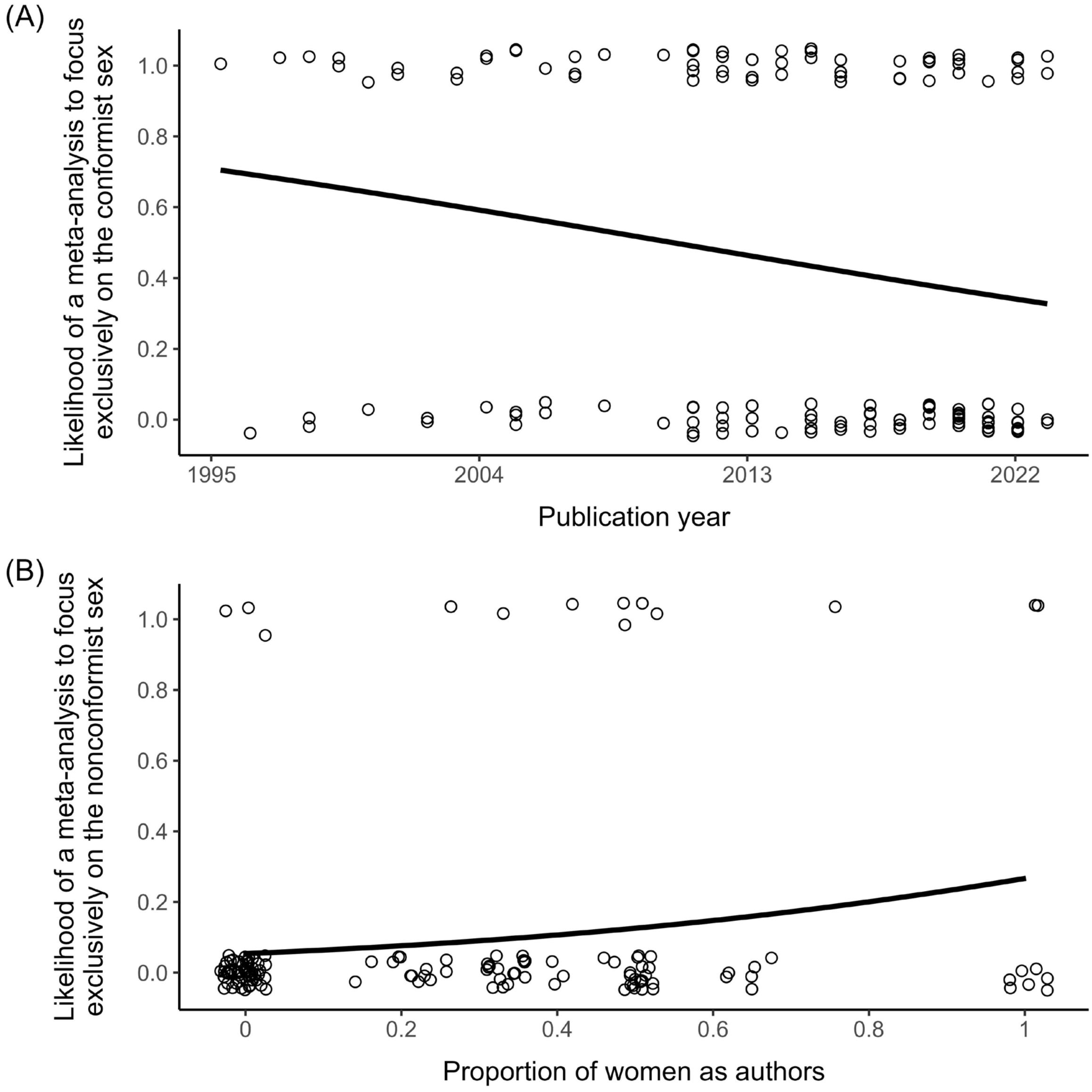

Figure 18. Relationship between the exclusive use of the conformist sex (mostly males) and publication year (A), and relationship between the exclusive use of the nonconformist sex (mostly females) and the proportion of women as authors (B) in meta-analyses on topics related to sexual selection. Solid lines represent the best fit from generalised linear models (Tables S17 and S19, respectively).

Surprisingly, we found that multiple authorship aspects were associated with meta-analyses' methodological transparency (Figure 19, Tables S20 and S21). Meta-analyses with proportionally more women as authors, with more continents listed as affiliations, and with the first affiliation from Europe, were more likely to be adequately transparent. It is difficult, however, to determine which specific factors could be driving this pattern, so here we can only speculate. For instance, it is possible that collaborations between authors based in different continents or intercontinental experiences of specific authors increase awareness to the importance of open research practices, encouraging them to be transparent in their work. Conversely, the greater challenges that women face in academia might pressure them to adhere to new practices faster than men if their work needs to show a higher quality standard than men's to be appreciated by their peers. Finally, as with previous analyses, overall transparency increased with meta-analyses' publication year (Figure 19C, Tables S20 and S21).

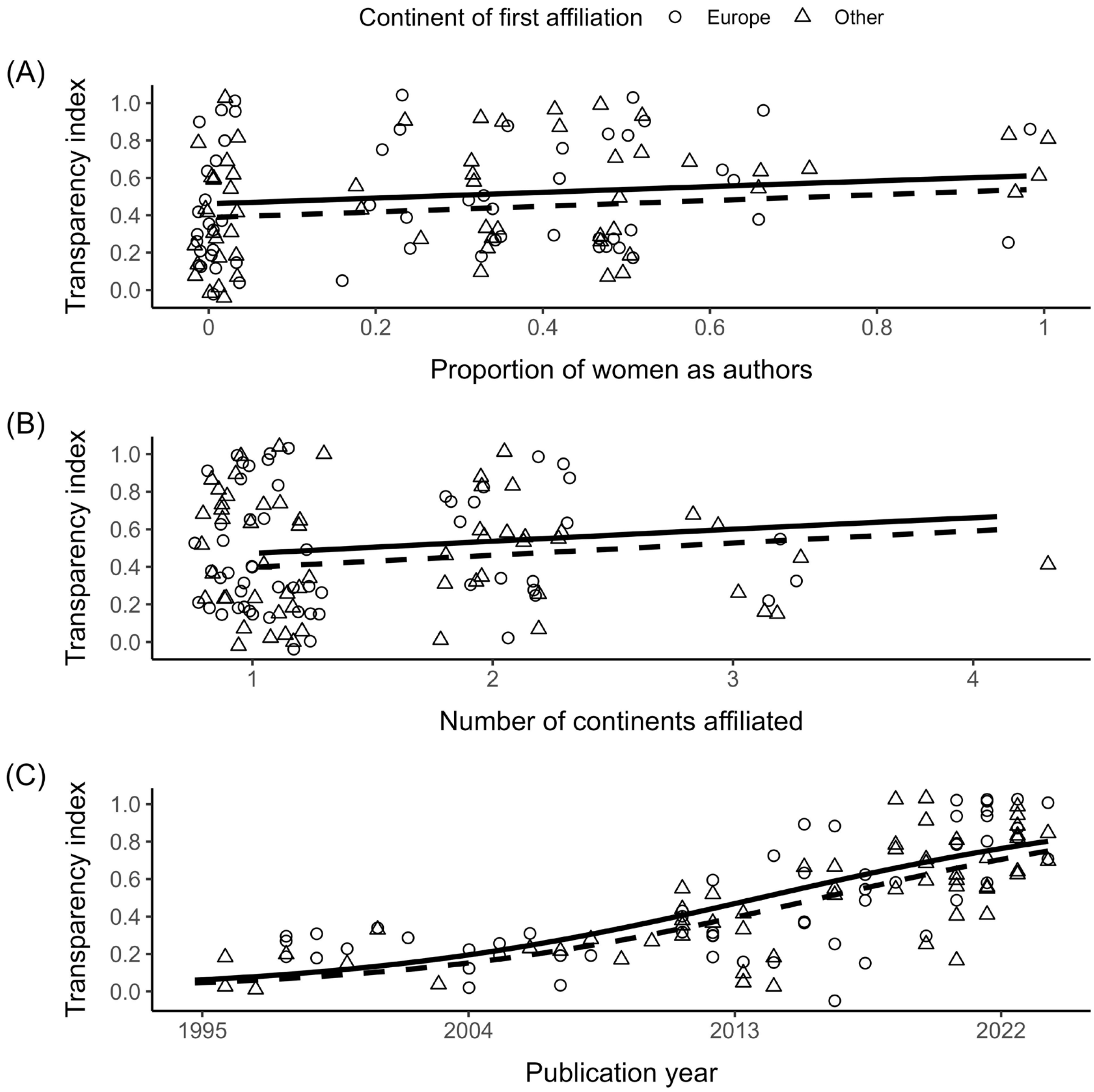

Figure 19. Relationship between methodological transparency and authorship aspects (A and B), or publication year (C) in meta-analyses on topics related to sexual selection. Solid and dashed lines represent the best fit from a generalised linear model for when the continent of the first affiliation reported in meta-analyses was Europe (circles) or another continent (triangles), respectively (Table S21).

(d) Importance of authorship diversity

Our bibliometric analysis suggests that authors conducting meta-analyses on topics associated with sexual selection are often men based in developed countries (see section III.4.a and section III.4.b), which is a pattern often found in academia (Astegiano, Sebastián-González & Castanho, 2019; Huang *et al.*, 2020). In addition, the international and intercontinental collaborations we found reiterate the globalisation of science (Gui, Liu & Du, 2019), although concentrated in the Global North (i.e. developed countries). We also found that important aspects regarding meta-analyses in our dataset, such as their taxonomic scope, focal sex, and methodological transparency, were associated with authorship diversity.

The biases we found regarding countries and gender are not limited to this specific literature, but simply another example of a more general problem in academia and research production overall. Yet, this does not mean we should accept this pattern idly. Rather, it emphasises that actions are needed to change this precarious situation as we found evidence (albeit correlational) that authorship diversity can promote positive changes in the literature (e.g. teams with proportionally more women produce more transparent meta-analyses). Even though we did not find evidence for the relationship between other authorship aspects with gaps in the secondary literature of sexual selection, diversity promotes creativity (McLeod, Lobel & Cox, 1996) and innovation (Nieto & Santamaría, 2007), ultimately being beneficial to science (Intemann, 2009; Cheruvelil *et al.*, 2014). The most obvious example of benefits brought by diversity in the context of meta-analyses comes from the inclusion of people with distinct language skills (e.g. from different countries) that can increase the coverage of the literature retrieved beyond just publications in English (Amano *et al.*, 2023). Furthermore, people of distinct nationalities can also vary in how they perceive stereotypes related to sexual behaviours in nature, making diverse teams more open to various perspectives (Pollo & Kasumovic, 2022).

While patterns of research production for countries follow economic trends (e.g. amount of public funding to research in each country; Gush *et al.*, 2018), social biases within academia also occur. For instance, as previously mentioned in section III.3.a, editors and reviewers made more favourable decisions for manuscripts authored by researchers from developed countries at an ecology journal (analyses controlled for language and quality of manuscripts; Fox, Meyer & Aimé, 2023; Srivastava *et al.*, 2024). On the other hand, gender inequity in research production can be explained by even more factors. First, it might be a consequence of a “leaky pipeline” that precludes women from filling higher academic positions as often as men (Shaw & Stanton, 2012; McDermott *et al.*, 2018). This is also seen in boards of scientific societies, in which women are outnumbered by men (Potvin *et al.*, 2018). Intuitively, this entails fewer opportunities for women to conduct or shape research. In addition, there is a gender gap in productivity (publication-based measures) in which women are outperformed by men, even in gender equal academic faculties (Astegiano *et al.*, 2019). This can be a consequence of differential pressures on women, compared with men, from inside (e.g. lower salary and more time spent in administrative tasks; DesRoches *et al.*, 2010) and outside (e.g. family caring; Fox, Fonseca & Bao, 2011) of academia.

Several solutions have been proposed to ameliorate these diversity issues. For instance, researchers from the Global North should actively and fairly collaborate with researchers from the Global South (see more suggestions in Haelewaters, Hofmann & Romero-Olivares, 2021 and in Nakamura *et al.*, 2023). Furthermore, many actions are being employed by different institutions to address gender disparity observed in academia, but they are rarely applied on a large scale or are ineffective (see Casad *et al.*, 2021 and references within). Yet, gender and country of affiliation or origin are just a few of several aspects that matter to diversity. For instance, people of colour (Evangelista *et al.*, 2020; Liu, Rahwan &

AlShebli, 2023) and from lower economic backgrounds (Lee, 2016) are commonly excluded from academia, revealing a need to develop ways to include these marginalised groups as well.

(7) Summarised recommendations

Conducting a meta-analysis on a topic related to sexual selection can be an arduous process. We summarise our recommendations for future work in the field of sexual selection, both for empiricists and researchers conducting meta-analyses, in Table 2 (see also Nakagawa *et al.*, 2017).

Table 2. Recommendations for meta-analytical research projects on topics related to sexual selection. Some of these recommendations can also be applied on projects with other methodological approaches in this field (in grey). FAIR stands for Findable, Accessible, Interoperable, Reusable (see Wilkinson *et al.*, 2016).

Item	**Summarised recommendations**	**Manuscript section(s)**
Research team	• Form diverse and inclusive research teams (e.g. gender equal) • Consider inviting researchers from the Global South for collaborations	III.6
Research question and scope	• Be mindful of the extent that certain taxa and topics related to sexual selection have received and your potential contribution to existing biases in the literature	III.2.a, III.2.e, III.3.a
	• Exclude humans as a study species if the synthesis also involves other animals	III.2.b
	• Avoid limiting (*a priori*) the study to only males (or only	III.2.f

	females for mate choice)	
	• Use the PECOS framework to formalise a research question • Be aware of the trade-offs from the chosen scope	III.3.b, III.5
Preregistration or protocol	• Develop a plan for the study and make it publicly available before conducting it	III.4.f
Data search	• Use different search sources (e.g. multiple databases), including grey literature • Provide search details, such as the dates on when it was conducted and the exact queries with Boolean operators used	III.4.a
Screening process	• Provide the number of retrieved, included, and excluded studies at every step of the screening process • Provide individual justification for study exclusions at the full-text screening stage • Make a PRISMA-like figure to summarise the screening process	III.4.b
Analysis	• Use appropriate software (e.g. R packages *metafor* or *MCMCglmm*) • Deal with statistical non-independence (e.g. from phylogeny and shared studies)	III.4.c
	• Quantify heterogeneity • Test for publication bias	III.4.e
	• Ensure that the meta-analytical model reflects the main question • Use moderators to explore sources of heterogeneity and to answer smaller questions	III.4.c, III.5
Code and data sharing	• Provide all data used in the study (preferentially in a separate FAIR file rather than in a table in the study) • Provide metadata for all data shared (in a separate file)	III.4.d

- Provide analysis scripts

IV. CONCLUSIONS

(1) The vastness of the field of sexual selection can be seen in more than 150 meta-analyses on topics associated with it. Although the first of these studies was published more than 25 years ago, most of them were conducted in the last decade.

(2) We found numerous biases in these meta-analytical studies. The majority focused on birds or insects (taxonomic bias) and on male traits or patterns (conforming sex bias). Furthermore, although the questions they asked were diverse, many concentrated on pre-copulatory sexual traits, such as weapons and ornaments. Thus, we call for greater research attention to females, underexplored animals (mostly invertebrates), and neglected topics such as post-copulatory processes.

(3) We argue that the conceptual gaps we identified can undermine scientific advancements related to sexual selection. Furthermore, we recommend to researchers to be careful with loose terms that are part of the sexual selection jargon to avoid confusion in meta-analyses in this field.

(4) The reporting quality of meta-analyses in the field of sexual selection is often poor, indicating that many might be unreliable or non-replicable. This problem is particularly strong for sharing of raw data and analysis scripts, revealing a dire need to improve these issues in future meta-analyses.

(5) We noticed that meta-analyses on topics related to sexual selection commonly employ approaches that are detrimental to their goals. We thus further recommend to authors to use global meta-analytical models with moderators to make inferences. This, however, should be

a consequence of a well thought plan that starts at the inception of the study, with a well formulated question and specific hypothesis.

(6) We observed both geographical and gender bias of researchers that conducted meta-analyses on topics related to sexual selection. Specifically, most of these studies were authored by men based in developed countries, signalling that gender and socio-cultural diversity might be lacking in the field of sexual selection.

(7) We found that distinct authorship aspects were related to the gaps we identified in the literature of sexual selection, especially regarding the participation of women. This reiterates the need for including underrepresented groups in academia.

(8) Despite our focus on meta-analyses, many of the issues and recommendations we pointed out can be extended to the primary literature (content) and to academia (authors). Thus, our manuscript possibly serves as a status report for the whole field of sexual selection.

V. ACKNOWLEDGEMENTS

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VI. AUTHOR CONTRIBUTIONS

Conceptualisation: P.P., M.L., S.N.; data curation: P.P.; formal analysis: P.P.; funding acquisition: S.N.; investigation: P.P., M.L., Y.Y., A.C., S.N.; methodology: P.P., M.L., S.N.; project administration: P.P., S.N.; software: P.P.; supervision: S.N.; visualisation: P.P.; writing - original draft: P.P., S.N.; writing - review & editing: P.P., M.L., Y.Y., A.C., S.N.

VII. DATA AVAILABILITY

The supplementary material is available at https://pietropollo.github.io/map_sexual_selection.

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