

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

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9

10 **ABSTRACT**

11 Sexual selection has been a popular subject within evolutionary biology because of its central  
12 role in explaining odd and counterintuitive traits found in nature. Consequently, the literature  
13 associated with this field of study became vast, with meta-analytical studies attempting to  
14 draw inferences from it. These meta-analyses have now accumulated, varying in scope and  
15 quality, thus calling for a synthesis of these syntheses. Here, we created a systematic map  
16 with a report appraisal of meta-analyses on topics associated with sexual selection, aiming to  
17 comprehend the conceptual and methodological gaps in this secondary literature. To further  
18 understand these gaps and their potential origins, we also conducted bibliometric analyses  
19 that identify the gender and origin of researchers that generated these studies. We included  
20 152 meta-analytical studies in our systematic map as a result of a systematic literature search.  
21 We found that most meta-analyses focused on males and on certain animal groups (e.g.  
22 birds), indicating severe sex and taxonomic biases. The topics in these studies greatly varied,  
23 from proximate (e.g. relationship of ornaments with other traits) to ultimate questions (e.g.  
24 formal estimates of sexual selection strength), albeit the former were more common. We also  
25 observed several common issues in these studies, such as lack of detailed information

26 regarding searches, screening, and analyses, which ultimately impairs the reliability of many  
27 of these meta-analyses. In addition, most of the meta-analyses' authors were men affiliated to  
28 institutions from developed countries, pointing to both gender and geographical authorship  
29 biases. Many of our findings might simply reflect patterns in the current state of the primary  
30 literature and academia, suggesting that our study can serve as an indicator of the issues  
31 within the field of sexual selection at large. Still, we provide both conceptual and analytical  
32 recommendations to improve future studies in the field of sexual selection, such as to avoid  
33 including humans with other animals in meta-analyses, to clarify traits of interest instead of  
34 simply using loosely defined lingo, and to properly match studies' questions and meta-  
35 analytical models.

36  
37

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

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95 **I. INTRODUCTION**

96 *(1) Background*

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

113 To be able to generalise results and advance science, one can combine knowledge  
114 from different individual investigations (Jennions *et al.*, 2012). Systematic reviews and meta-  
115 analysis are considered the gold standard for such comprehensive evidence synthesis  
116 (Koricheva, Gurevitch & Mengersen, 2013; Borenstein *et al.*, 2021). This is because  
117 systematic reviews aim to detect all the studies conducted on a certain topic, while meta-  
118 analyses additionally provide quantitative measures related to the average and dispersion of  
119 studies' outcomes by standardising (effect sizes) and weighting them by their precision

120 coupled with solid statistical techniques (Jennions *et al.*, 2012; Gurevitch *et al.*, 2018;  
121 Borenstein *et al.*, 2021). It is unsurprising then that several meta-analyses have been  
122 conducted to test long standing hypotheses of topics relevant to sexual selection. Jennions *et*  
123 *al.* (2012) reviewed some of these meta-analyses, summarised their content, and identified  
124 opportunities for future synthesis studies. Yet, many other meta-analyses in this field have  
125 accumulated during the more than a decade since Jennions *et al.* (2012), suggesting that a  
126 new audit of the knowledge provided by these studies is warranted. This can be achieved with  
127 a systematic map, which is a tool that synthesises research on a broad topic in a user-friendly  
128 format (Miake-Lye *et al.*, 2016; O’Leary *et al.*, 2017; Sutherland & Worldley, 2018).

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

140         Bibliometrics represents another set of tools that can improve our understanding of a  
141 field and its patterns. That is because bibliometrics provide quantitative information on  
142 authors and collaborative networks. Such information could be used to improve gender and  
143 geographical representation of research topics, addressing issues around equity, diversity, and  
144 inclusiveness (Davies *et al.*, 2021). Traditionally, systematic reviews (and maps)

145 concentrated on the existing research content, avoiding discussions on who conducted it  
146 (Nakagawa *et al.*, 2019). Yet, given historic conceptual ‘male-centeredness’ in the topic of  
147 sexual selection (Ah-King, 2022), it may be of particular importance to examine the diversity  
148 and inclusiveness of authors of meta-analyses related to sexual selection. To our knowledge,  
149 this has never been done for sexual selection research, uncovering an exciting opportunity for  
150 this field.

151

## 152 (2) Objectives

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

- 159 1. What is the scope of existing meta-analyses?
  - 160 1. Where are the gaps in the evidence syntheses, requiring more attention or  
161 updates? See section III.2
  - 162 2. Which specific questions have been addressed? See section III.5.
  - 163 3. What are the challenges in this field and how to address them? See section  
164 III.6.
- 165 2. How transparent and robust are existing meta-analyses? See section III.3.
- 166 3. Who and from where are researchers that conducted existing meta-analyses? See  
167 section III.4.

168

169 **II. METHODS**

170 Our methodology was described in our pre-registration (Pollo *et al.*, 2023), and we adhered to  
171 it as much as possible. However, we adjusted several elements to improve the manuscript.  
172 These adjustments are mentioned throughout the manuscript when applicable. We broadly  
173 followed the guidelines of ROSES for reporting of systematic maps (Table S1; Haddaway *et*  
174 *al.*, 2018).

175

176 *(1) Literature searches*

177 We conducted literature searches using six different sources, all on March 15th, 2023. First,  
178 we conducted a main database search using Scopus and Web of Science (Core Collection),  
179 both accessed through the University of New South Wales, Sydney. For this, we created  
180 strings with keywords aimed to capture meta-analytical studies on non-human animals that  
181 cover one or more topics relevant to sexual selection (see Supplementary material and section  
182 II.2). Second, we retrieved the backward and forward citations from Jennions *et al.* (2012)  
183 (i.e. list of citations and papers that cited it, respectively). Third, to find relevant grey  
184 literature, we used a simplified keyword string (“meta-analysis” AND “sexual selection”) in  
185 Bielefeld Academic Search Engine (BASE), filtering only theses (doctype:18\*). Fourth, we  
186 conducted several searches in Google Scholar using translations of the string used in BASE  
187 in Simplified and Traditional Chinese, Croatian, Japanese, Polish, Portuguese, Russian, and  
188 Spanish (see Supplementary material for details). However, we only screened the ten first  
189 results from each of these Google Scholar searches, sorted by relevance. We planned to  
190 screen 10 more if at least half of the previous 10 contained relevant articles, but that was not  
191 the case for any language. Additionally, we manually included four studies that were not  
192 captured by our searches (Janicke *et al.*, 2018; Aguiar Del Matto, 2018; Gómez-Llano *et al.*,  
193 2023; Dougherty, 2023). A pilot conducted for our pre-registration (see Pollo *et al.* 2023)



194 found that these searches retrieved relevant benchmark articles, ensuring that our searches  
195 were comprehensive.

196

197 (2) *Screening process and inclusion criteria*

198 Our screening criteria were summarised in Table 1 (but see details in the Supplementary  
199 material), while our screening process is shown in Figure 1 (slightly different from the one in  
200 our pre-registration but conceptually identical; see Pollo *et al.* 2023). We used Rayyan QCRI  
201 (Ouzzani *et al.*, 2016) for both of our initial and full-text screenings. ML and PP  
202 independently conducted the initial screening, i.e. assessed the title, abstract, and key-words  
203 of retrieved papers. The full-text content of studies that passed this initial screening were then  
204 independently assessed by PP and either AC, ML, SN, or YY (in roughly 29%, 14%, 28%,  
205 and 29% of the cases, respectively). In both initial and full-text screening, authors solved  
206 conflicts through discussion until consensus was reached.

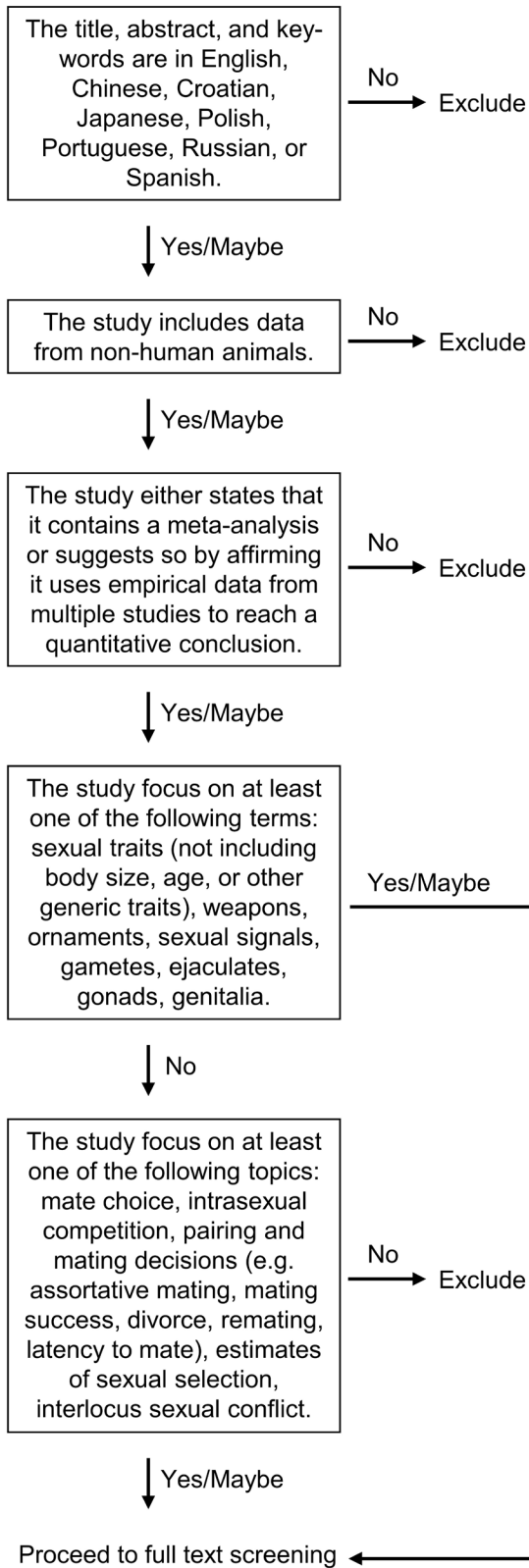
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208 Table 1. Scope of our systematic map of meta-analyses on topics related to sexual selection,  
209 according to the PECOS framework.

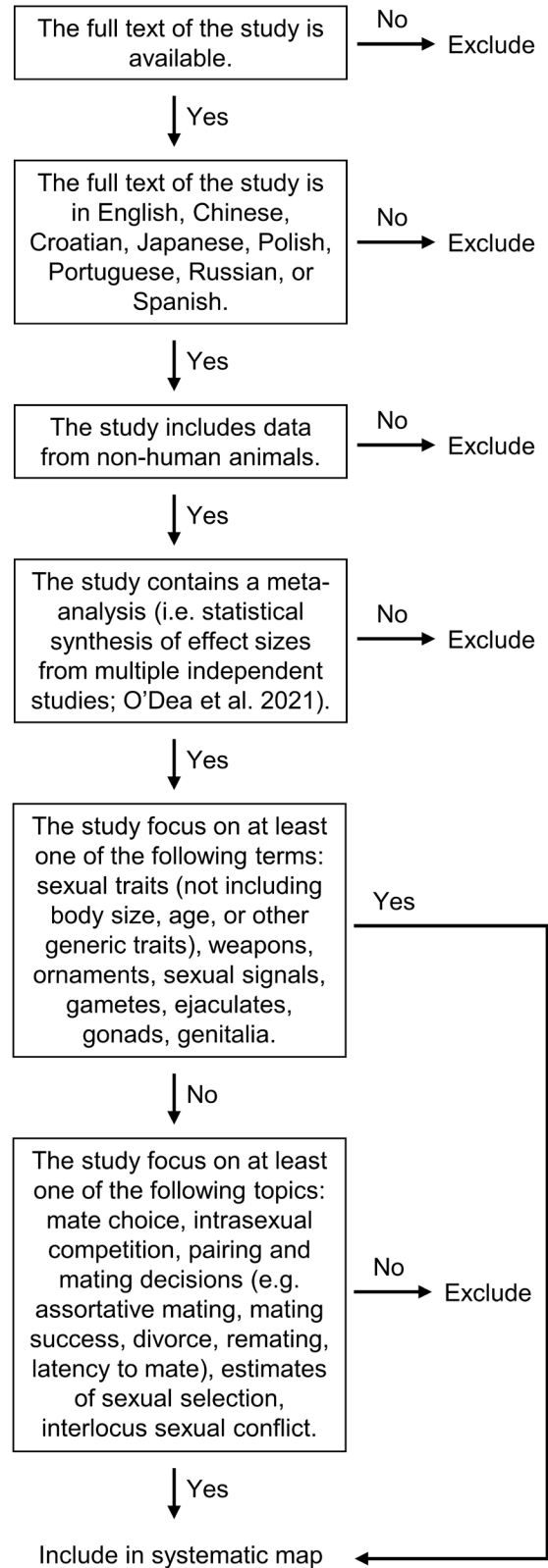
<b>Population</b>	Non-human animals (occasionally other organisms as well if they are included in meta-analyses with non-human animals)
<b>Exposure</b>	Factors that potentially affect mechanisms and patterns related to sexual selection.
<b>Comparator</b>	Not applicable.
<b>Outcomes</b>	Related to patterns 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.
<b>Study-design</b>	Meta-analyses ( <i>sensu</i> O’Dea <i>et al.</i> 2021: statistical synthesis of effect sizes from multiple independent studies).

210

### A) Initial screening



### B) Full-text screening



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

215

### 216 (3) *Data extraction*

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

220

#### 221 (a) Systematic map

222 We extracted data from papers included in our study in respect to the scope of their research  
223 questions, as well as specific aspects of the data they used in respect to taxa, focus sex, and  
224 methodological approach. To do this, we used a Google Form questionnaire for each paper  
225 (Table S3). We modified the way we summarised questions from each study from our initial  
226 plan to best fit our classification system presented on our systematic map (see sections III.2.e  
227 and III.5). Several aspects made the task of describing and classifying questions from meta-  
228 analytical studies complex and subjective (see also section III.6.c). For instance, not all  
229 questions from included papers were relevant to our systematic map (e.g. Goldberg *et al.*,  
230 2020) contained questions related to paternal care). Similarly, not all variables used within  
231 certain questions were relevant (e.g. Leung & Forbes, 1996) mixed mating success with other  
232 fitness measures). Therefore, we selected and described the studies' questions relevant to our  
233 systematic map without necessarily relying on the exact words used by their original authors  
234 (see further details in Supplementary material). We aimed to extract only questions that we  
235 considered central to each meta-analytical study. Because of this, we modified or excluded  
236 some variables initially extracted (e.g. how main questions were answered; see also section

237 III.6.c). Furthermore, we described studies' questions without mentioning the taxa or sex  
238 investigated when possible, as we discuss these issues separately (sections III.2.a and III.2.f).  
239 Moreover, we intentionally discussed meta-analyses' questions without mentioning their  
240 results because one of our goals was to show that many of their findings can be problematic  
241 due to conceptual and methodological reasons (sections III.3 and III.6).

242 One particular information that we collected from meta-analyses included in our  
243 systematic map was the sex of individuals that were used to extract effect sizes (discussed in  
244 section III.2.f). However, our analysis related to this information was made at the level of the  
245 questions extracted from meta-analyses (as in section II.2.e) rather than studies. We  
246 ultimately classified these meta-analytical questions based on the stereotypes proposed by the  
247 idea of sex roles (following Pollo & Kasumovic, 2022). For instance, meta-analytical  
248 questions that focused exclusively on males and their traits were deemed "conforming" to the  
249 idea of sex roles that poses males as competitive and as the usual sex under sexual selection  
250 (Ah-King & Ahnesjö, 2013). Conversely, meta-analytical questions that focused exclusively  
251 on females and their traits were classified as "nonconforming" to the idea of sex roles, which  
252 poses females as coy (Ah-King & Ahnesjö, 2013). The only exception for this classification  
253 was for meta-analytical questions that fitted into the mate choice category (see section  
254 III.5.d), in which exclusive focus on females was considered conformist, and exclusive focus  
255 on males was nonconformist, as the idea of sex roles proposes that females are choosy while  
256 males are unselective (Ah-King & Ahnesjö, 2013). Furthermore, meta-analytical questions  
257 that focus on both males and females were classified as "neutral".

258

#### 259 (b) Reporting appraisal

260 We used PRISMA-EcoEvo (O'Dea *et al.*, 2021) to evaluate reporting and methodological  
261 aspects of meta-analyses included in our systematic map. Although PRISMA-EcoEvo only

262 provides guidelines and is not an appraisal tool, other appraisal tools (e.g. Woodcock, Pullin  
263 & Kaiser, 2014: CEESAT; Shea *et al.*, 2017: AMSTAR 2) do not include items we aimed to  
264 quantify. Therefore, we used the PRISMA-EcoEvo checklist for reporting appraisal, choosing  
265 a subset of the items that are often deemed key aspects for transparency and robustness of  
266 meta-analyses, such as registering planned research (Allen & Mehler, 2019), detailing the  
267 search and screening of studies (McGowan *et al.*, 2016; Palpacuer *et al.*, 2019), handling  
268 statistical non-independence (Noble *et al.*, 2017), and sharing data (Piccolo & Frampton,  
269 2016), among others (see section III.3). We mainly surveyed whether these elements were  
270 described or provided, but for specific aspects we also collected detailed information if  
271 possible (e.g. which software was used for statistical inferences). Moreover, although our  
272 systematic map included meta-analyses in a broad sense (see section II.2), some may be more  
273 restrictive on meta-analyses' definition (Nakagawa *et al.*, 2023a). Thus, we also verified  
274 whether studies included in our systematic map were traditional meta-analyses, i.e. used  
275 traditional effect sizes and properly modelled heterogeneity using additive weighting  
276 (Nakagawa *et al.*, 2023a). We primarily assessed this information based on statistical  
277 methods described in studies, including model equations and software used.

278

### 279 (c) Bibliometrics

280 We extracted author affiliations and names from meta-analyses on topics associated with  
281 sexual selection. We retrieved this information from Scopus using the packages *bibliometrix*  
282 (Aria & Cuccurullo, 2017) and *rscopus* (Muschelli, 2019) in R (R Core Team, 2022), on  
283 August 7th and 14th 2023, respectively. We manually extracted this information for studies  
284 that were not yet indexed in Scopus (e.g. theses and recent papers,  $n = 9$ ). We then  
285 determined authors' gender from their first name using the package *genderizeR* (Wais, 2016).  
286 Although this approach has its faults (e.g. erroneous label assignment, especially for people

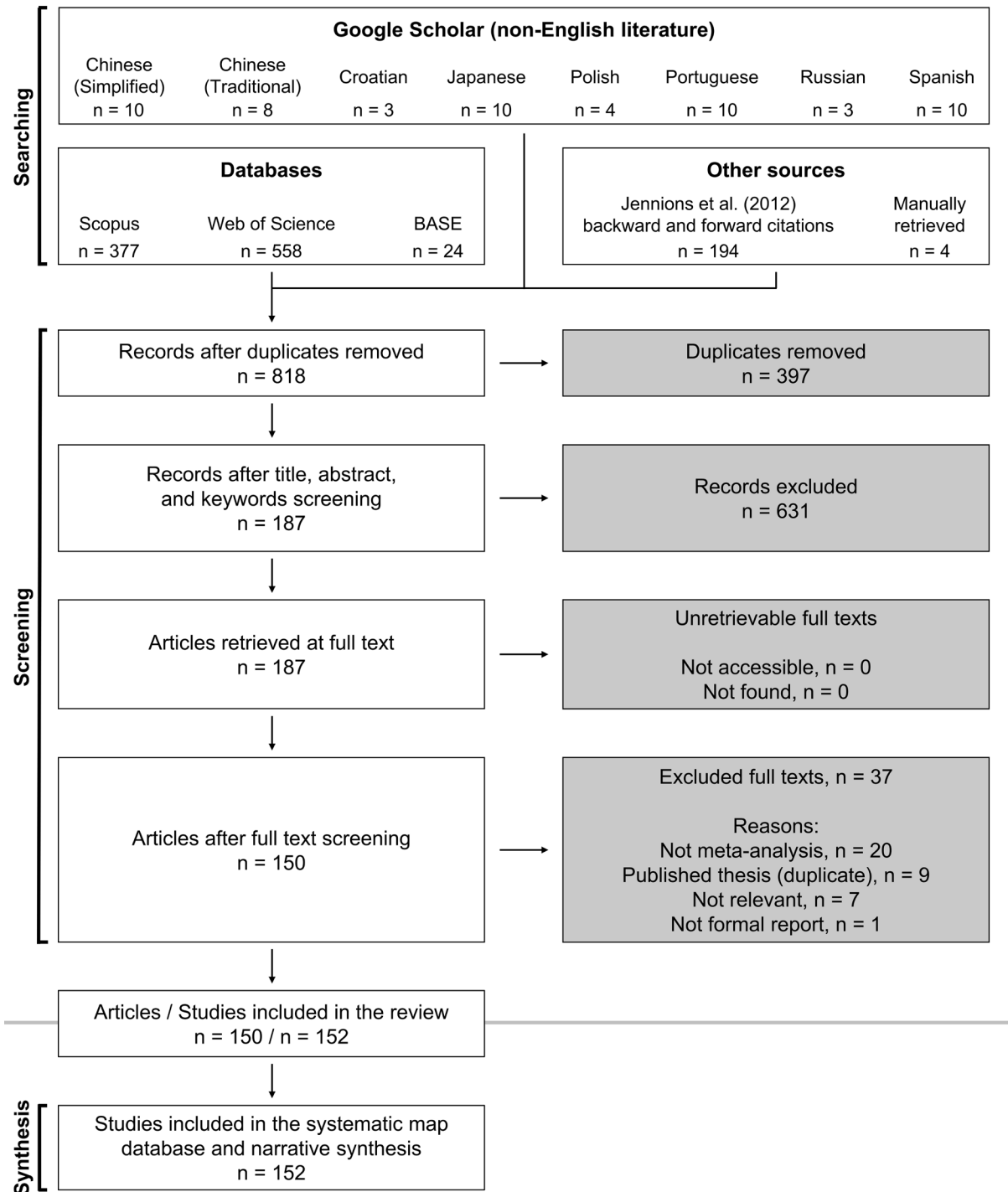
287 that do not identify with binary genders), it includes an estimation of the certainty that a name  
288 is associated with a given gender based on real data. Thus, to minimise errors, we only used  
289 this automatic labelling when the gender assignment certainty was higher than 95%. For  
290 names with ambiguous gender association (i.e. lower certainty), we manually searched the  
291 authors' name online to assign gender based on information we could find (e.g. profiles on  
292 universities' websites).

293

### 294 **III. RESULTS AND DISCUSSION**

#### 295 *(1) Number of eligible meta-analytic studies*

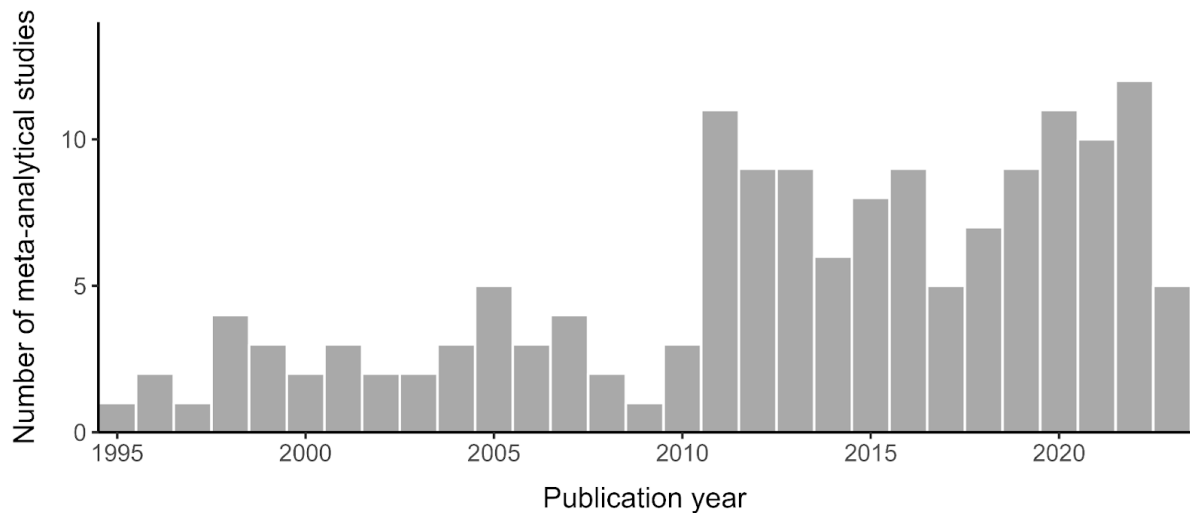
296 Our screening process is summarised in Figure 2. Searches from all sources retrieved a total  
297 of 1,215 records, although 397 of them were duplicates. We thus assessed the title, abstract,  
298 and keywords of the remaining 818 articles, from which 187 met our initial selection criteria  
299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



310

311 Figure 2. ROSES flow chart of the screening process.

312



313

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

317

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

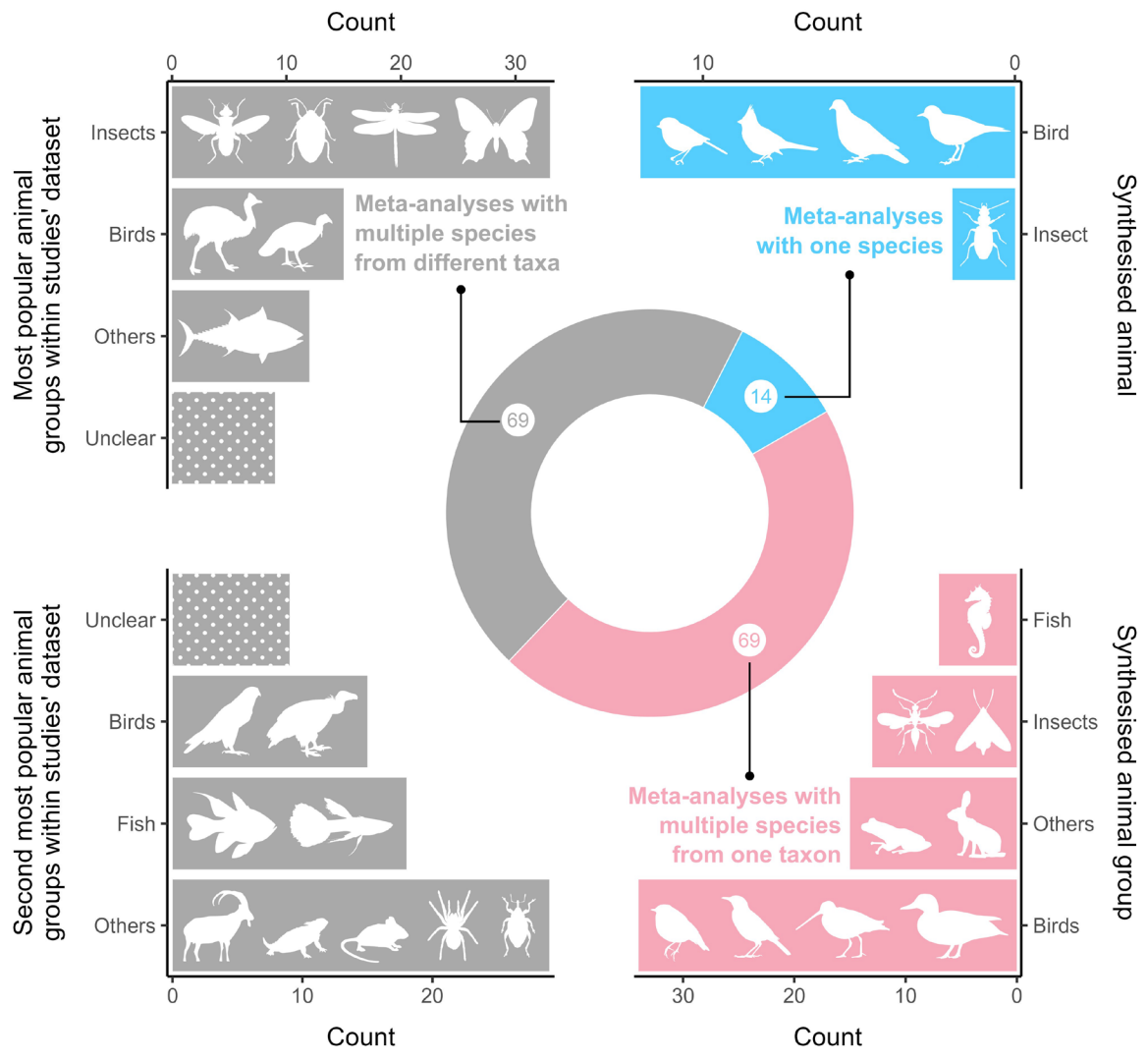
319 (a) Taxonomic groups

320 We verified which animal groups (at the taxonomic class level) were synthesised by the  
 321 meta-analyses included in our systematic map (Figure 4). We found that more than half of all  
 322 of these meta-analyses (83 out of 152; 54.6%) limited their scope to a single species (n = 14)  
 323 or to a specific taxonomic group (n = 69), while the remaining ones (n = 69; 45.4% of the  
 324 total) did not apply taxonomic filters (i.e. all animal species could be included). We then  
 325 identified the animal groups investigated by these meta-analyses, although we could not  
 326 obtain relevant details from nine of them (all taxonomically unrestricted meta-analytical  
 327 studies). Birds were by far the most popular animal group observed in our systematic map: 12  
 328 out of 14 (85.7%) single species meta-analyses focused on a bird species, 34 out of 69  
 329 (49.3%) specific taxonomic group meta-analyses focused exclusively on birds, and 30 out of  
 330 60 (50%) taxonomically unrestricted meta-analyses for which we obtained taxonomic details



331 showed birds as the first or second most copious group in number of species included in these  
332 studies (Figure 4). Insects followed behind, as 2 out of 14 (14.3%) single species meta-  
333 analyses focused on an insect species, 13 out of 69 (18.8%) specific taxonomic group meta-  
334 analyses focused exclusively on insects, and 47 out of 60 (78.3%) taxonomically unrestricted  
335 meta-analyses for which we obtained taxonomic details showed insects as the first or second  
336 most copious group in number of species included in these studies (Figure 4). However, note  
337 that the actual proportion of species that first or second most popular animal groups represent  
338 in taxonomically unrestricted meta-analyses tends to decrease with the total number of  
339 species used by a meta-analysis (Figure 5). For instance, Soper, Ekroth & Martins (2021)  
340 extracted data from nine species in their study, eight of them being insects and one being a  
341 mammal, meaning that the two most abundant animal groups in the study represented all its  
342 taxonomic diversity. In contrast, Rios Moura *et al.* (2021) included 341 species, 21.1% birds  
343 and 20.8% insects, so that these two groups comprised only less than half of the species  
344 represented in the study.

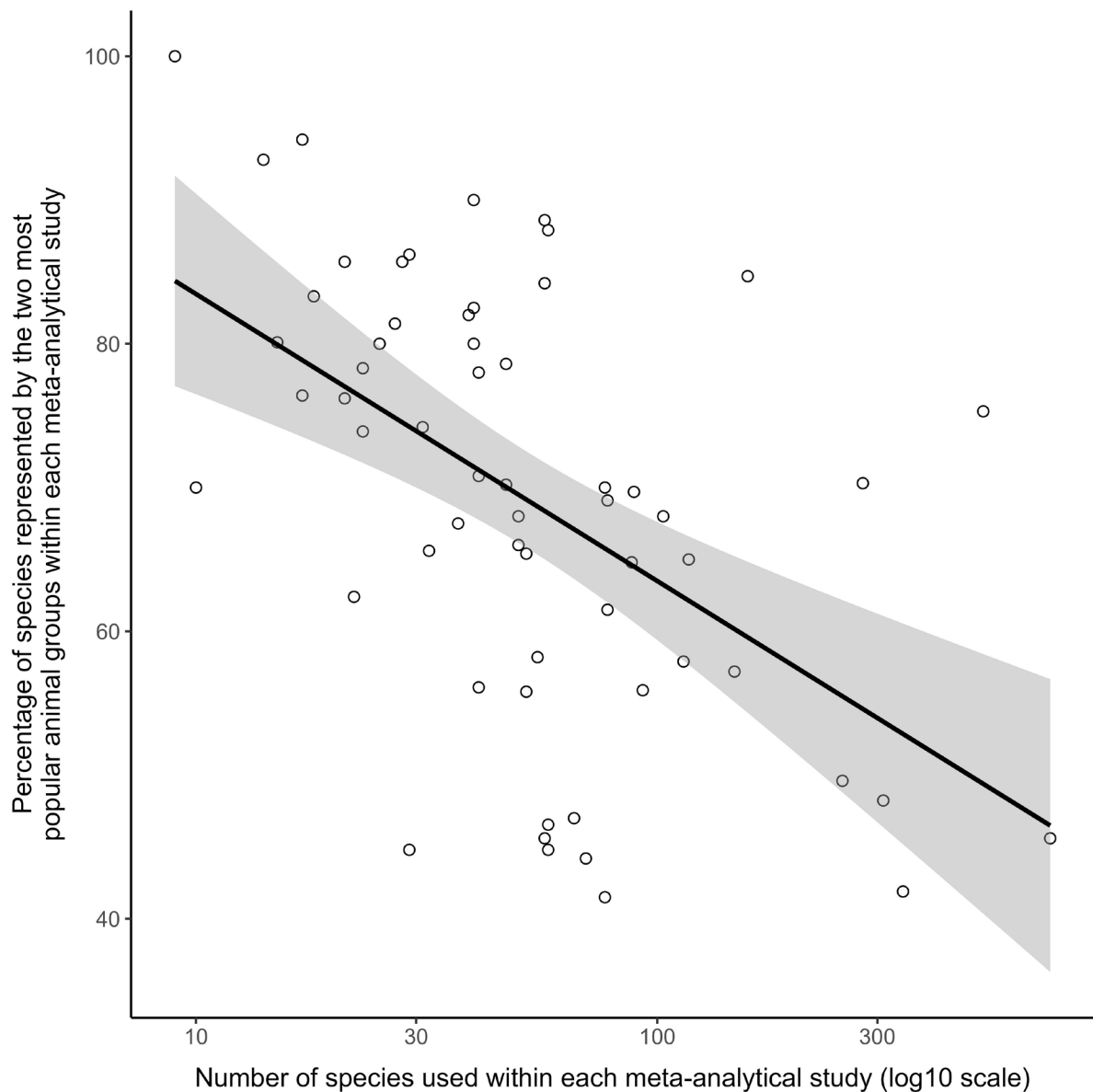
345



346

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

350



351

352 Figure 5. Relationship between the logarithm of the number of species used by meta-  
 353 analytical studies with multiple species from different taxa and the percentage of species  
 354 represented by the two most abundant animal groups in these studies.

355

356 Our findings are similar to studies that investigated taxonomic coverage in empirical  
 357 research outputs from sexual selection (Zuk *et al.*, 2013), but also from other biological fields  
 358 and subfields, such as animal behaviour (Rosenthal *et al.*, 2017; see also Owens, 2006),  
 359 animal ecology (Bonnet, Shine & Lourdais, 2002), parental care (Stahlschmidt, 2011),

360 biodiversity (Troudet *et al.*, 2017), and conservation (Seddon, Soorae & Launay, 2005). Akin  
361 to our results, all of these studies found that some taxonomic groups (usually birds) receive  
362 much more research attention than others, revealing taxonomic bias. Yet, our findings  
363 represent only the tip of this problematic iceberg, as the sole taxonomic information we  
364 extracted from meta-analyses was taxonomic class. As Zuk *et al.* (2013) showed, taxonomic  
365 bias is insidious as it occurs at the genus and species level as well. For example, most meta-  
366 analyses that include insects have many of their effect sizes from fruit flies (*Drosophila*) and  
367 other model species (e.g. de Boer *et al.*, 2021).

368 Taxonomic bias might stem from distinct sources, such as organisms'  
369 conspicuousness and easiness to access (Murray *et al.*, 2015; Yarwood, Weston & Symonds,  
370 2019; Ellison *et al.*, 2021), common human attitudes towards specific animals (e.g. Bjerke &  
371 Østdahl, 2004), frequent use of certain organisms whose experimental techniques are well  
372 established (i.e. model systems, Zuk *et al.*, 2013), or previous experience with research on a  
373 given animal group (Pollo & Kasumovic, 2022). However, accumulating knowledge on only  
374 a fraction of the existing animal diversity severely limits our generalisation ability, making  
375 this taxonomic hyper focus extremely detrimental to our understanding of natural processes.  
376 Surprisingly, it seems that little has been done since the first reports of taxonomic bias more  
377 than two decades ago (Bonnet *et al.*, 2002), stressing that solutions to this issue (e.g.  
378 incentivizing research on data deficient animal groups at both low and high taxonomic levels)  
379 remain urgent.

380

### 381 (b) Inclusion of humans

382 Our systematic map deliberately required that meta-analytical studies had to explore non-  
383 human animals to be included (see section II.2). Yet, humans could be used along other  
384 species in these meta-analyses. We found that 18 studies from our systematic map included

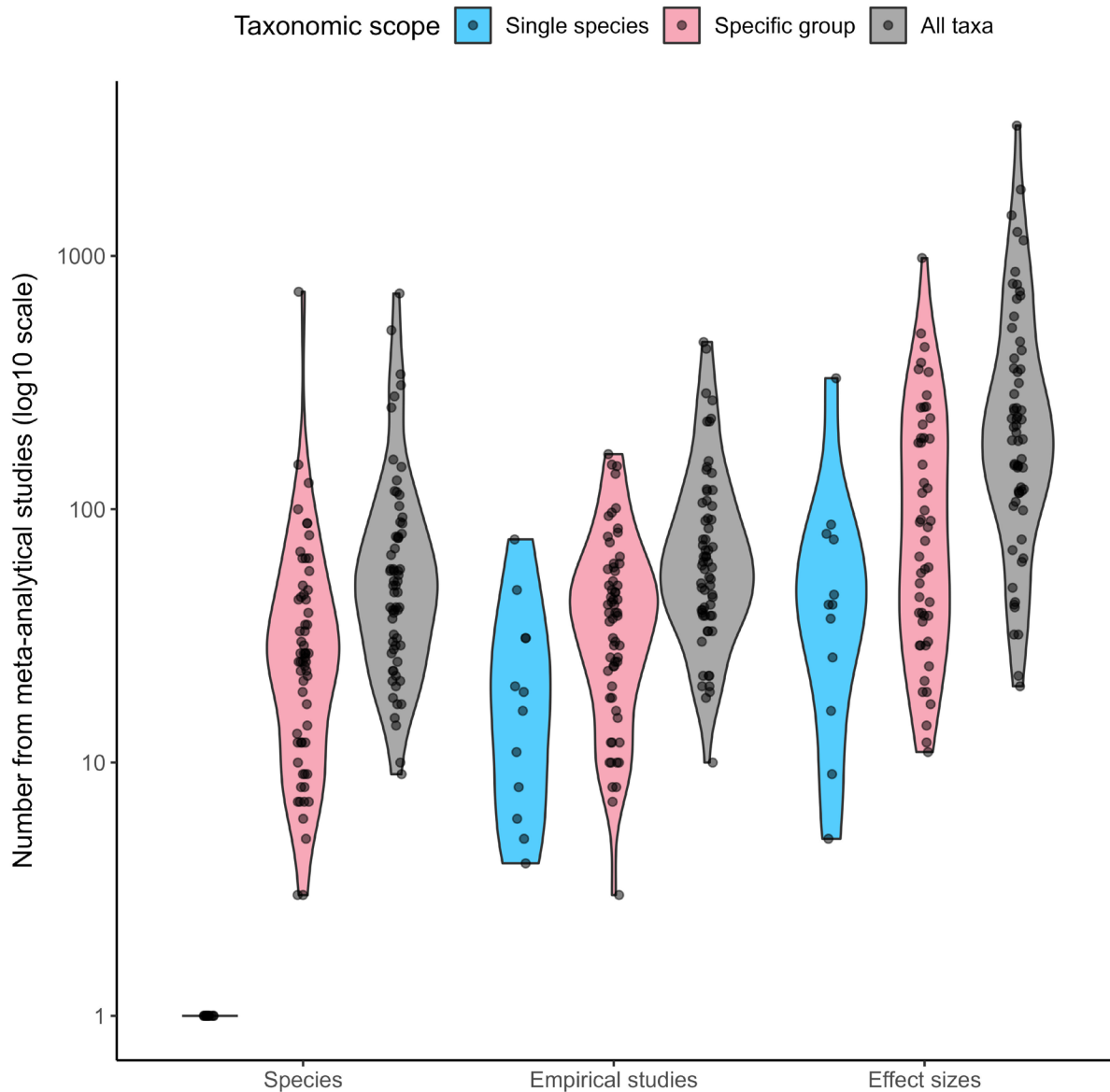
385 humans, albeit this number can be higher given that another three studies were unclear  
386 regarding this information. Although this number seems low, it represents almost a quarter of  
387 studies with relevant taxonomic scope (only 75 studies did not exclude primates *a priori*, see  
388 section III.2.a). Even though mixing humans with other animals in meta-analyses related to  
389 sexual selection can be taken as a matter of preference, we discuss the potential issues arising  
390 from this decision later in the manuscript (see section III.6.a).

391

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

393 When possible, we extracted the number of effect sizes, species, and empirical studies used in  
394 meta-analyses on sexual selection related topics. At least one of these numbers was not  
395 explicitly provided in 38 (25%) meta-analytical studies. Furthermore, we extracted these  
396 numbers manually from tables or data files (rather than from what was explicitly reported in-  
397 text) in 57 meta-analyses, highlighting the lack of transparent reporting of important  
398 methodological details in meta-analyses in the field. We found that the number of empirical  
399 studies, effect sizes, and species increased with taxonomic scope (Figure 6). Along with  
400 taxonomic distribution of the data, these numbers are pivotal to address generality limitations  
401 in meta-analyses (Spake *et al.*, 2022). However, they are rarely provided. For instance,  
402 although Cally, Stuart-Fox & Holman (2019) used a total of 459 effect sizes from 65  
403 empirical studies (both numbers mentioned in-text), these were related to only 15 species.  
404 Yet, the authors did not mention this low number of species and did not discuss the impacts  
405 of relying on such a limited taxonomic dataset to make a statement for the entire animal  
406 kingdom. This often appears as a symptom of a neoliberal academia (Lorenz, 2012), which  
407 pushes researchers to publish in high impact factor journals that require bold claims,  
408 stimulating the concealment of weaknesses to increase significance.

409



410

411 Figure 6. Number of effect sizes, species, and empirical studies found in meta-analytical  
 412 studies (logarithmic scale) on topics related to sexual selection depending on their taxonomic  
 413 scope.

414

415 (d) Study design

416 Briefly stating the design employed by selected empirical studies (experiments or field  
 417 observations) represents the bare minimum of transparency from meta-analyses. Yet, we  
 418 found that almost 40% (n = 60) of the meta-analytical studies from our systematic map were

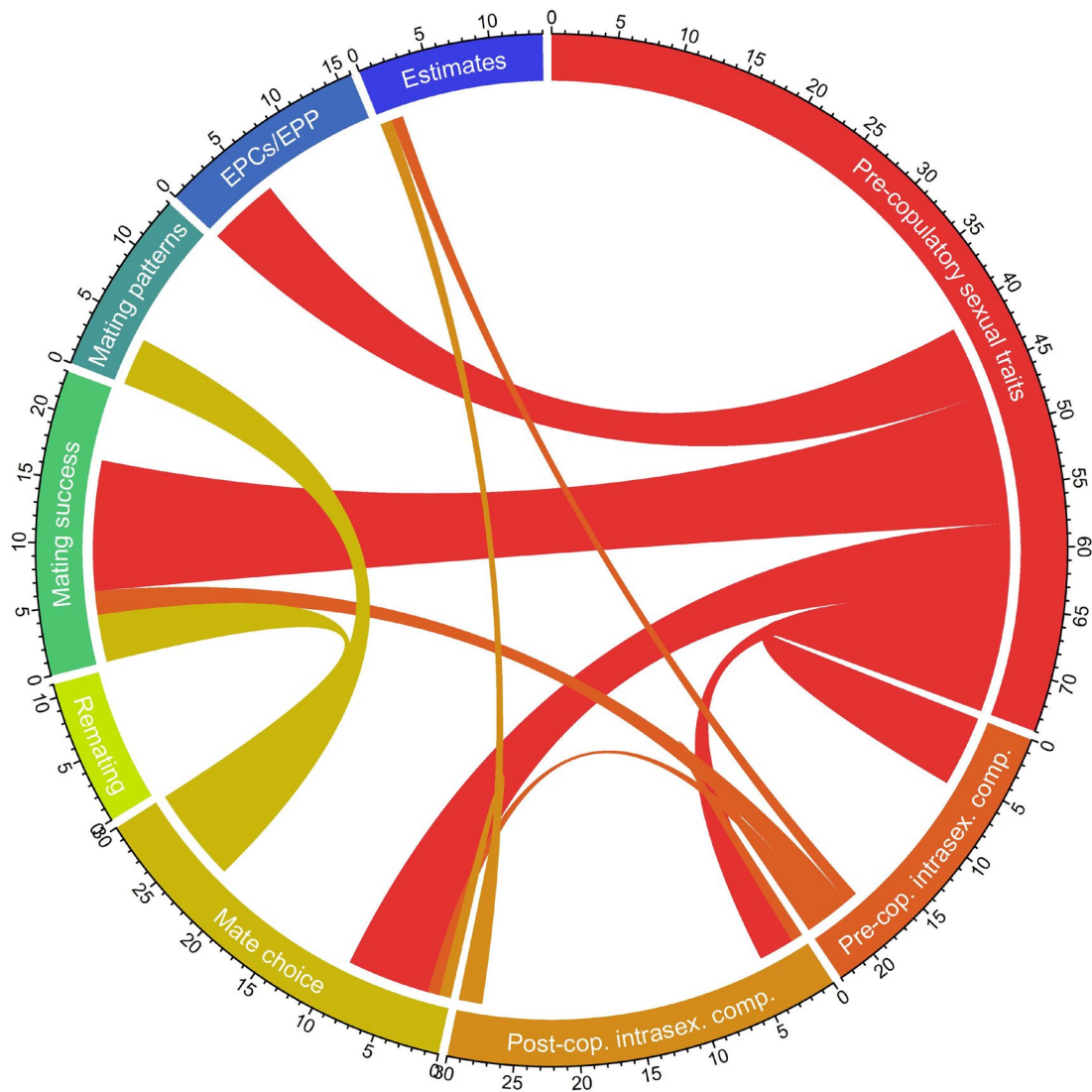
419 unclear about this information. From those that specified this information ( $n = 92$ ), 13  
420 exclusively used field observations, 32 exclusively used experimental investigations, while  
421 47 combined both of these designs. A comprehensive description of included studies'  
422 methodology is ideal as it helps meta-analyses' readers to identify some of their limitations  
423 (Page *et al.*, 2021). This is because observations and experiments can have multiple  
424 peculiarities and vary in the degree of variables controlled, especially when distinct  
425 organisms require methodological adjustments. The design type selected by a meta-analysis  
426 has direct impacts on what is in fact being evaluated. For instance, to attest mate choice one  
427 needs to isolate several variables (e.g. number of individuals present; see section III.5.d), so  
428 field observations are much less reliable. Mixing approaches is fine as long as authors use  
429 moderators to distinguish one design from another (e.g. mate choice experiments vs. mating  
430 success observations), which is another aspect missing in many meta-analyses in the field of  
431 sexual selection.

432

#### 433 (e) Overview of topics related to sexual selection

434 We extracted a single research question from most meta-analytical studies ( $n = 129$ , ca. 85%)  
435 and two to four research questions from the remaining 23 (ca. 15%), resulting in a total of  
436 187 research questions. Figure 7 illustrates the number of questions in each of the categories  
437 (i.e. topics connected to sexual selection) we created to classify meta-analytical questions: (1)  
438 pre-copulatory sexual traits, (2) pre-copulatory intrasexual competition, (3) post-copulatory  
439 intrasexual competition, (4) mate choice, (5) remating and eagerness to mate, (6) mating  
440 success, (7) mating patterns, (8) divorce and extra-pair patterns, and (9) sexual conflict and  
441 estimates of sexual selection. We assigned up to two topics we deemed most relevant to  
442 individual questions rather than to studies (but see Supplementary material). This resulted in  
443 138 questions associated with a single topic and 49 of them associated with two topics

444 (visualised as links between categories in Figure 7). Details of what each category within our  
 445 classification framework encompass are given and discussed in section III.5.  
 446



447  
 448 Figure 7. Number of meta-analytical questions for each topic related to sexual selection.  
 449 Links represent questions that fit into two topics. Topics (clockwise, red to blue): pre-  
 450 copulatory sexual traits, pre-copulatory intrasexual competition and associated traits, post-  
 451 copulatory intrasexual competition and associated traits, mate choice, remating and eagerness



452 to mate, mating success, mating patterns, divorce and extra-pair patterns (EPCs/EPP), sexual  
453 conflict and estimates of sexual selection.

454

455 (f) Focal sex

456 Studies with sex roles conformist (i.e. that focus only on males, except for questions on mate  
457 choice) and neutral approaches dominate meta-analyses related to sexual selection (Figure 8).

458 A single study exclusively focused on hermaphrodite animals (Graham *et al.*, 2015), and 14  
459 studies did not clarify the sex of individuals they focused on for any of their questions. Non-

460 conformist approaches only preponderate over others on questions regarding remating and  
461 eagerness to copulate, as studies on this topic essentially tested the benefits and costs of

462 polyandry (see section III.5.e). Conversely, questions on mating patterns are more sex-neutral  
463 than others, but this might simply reflect their inherent approach using data from

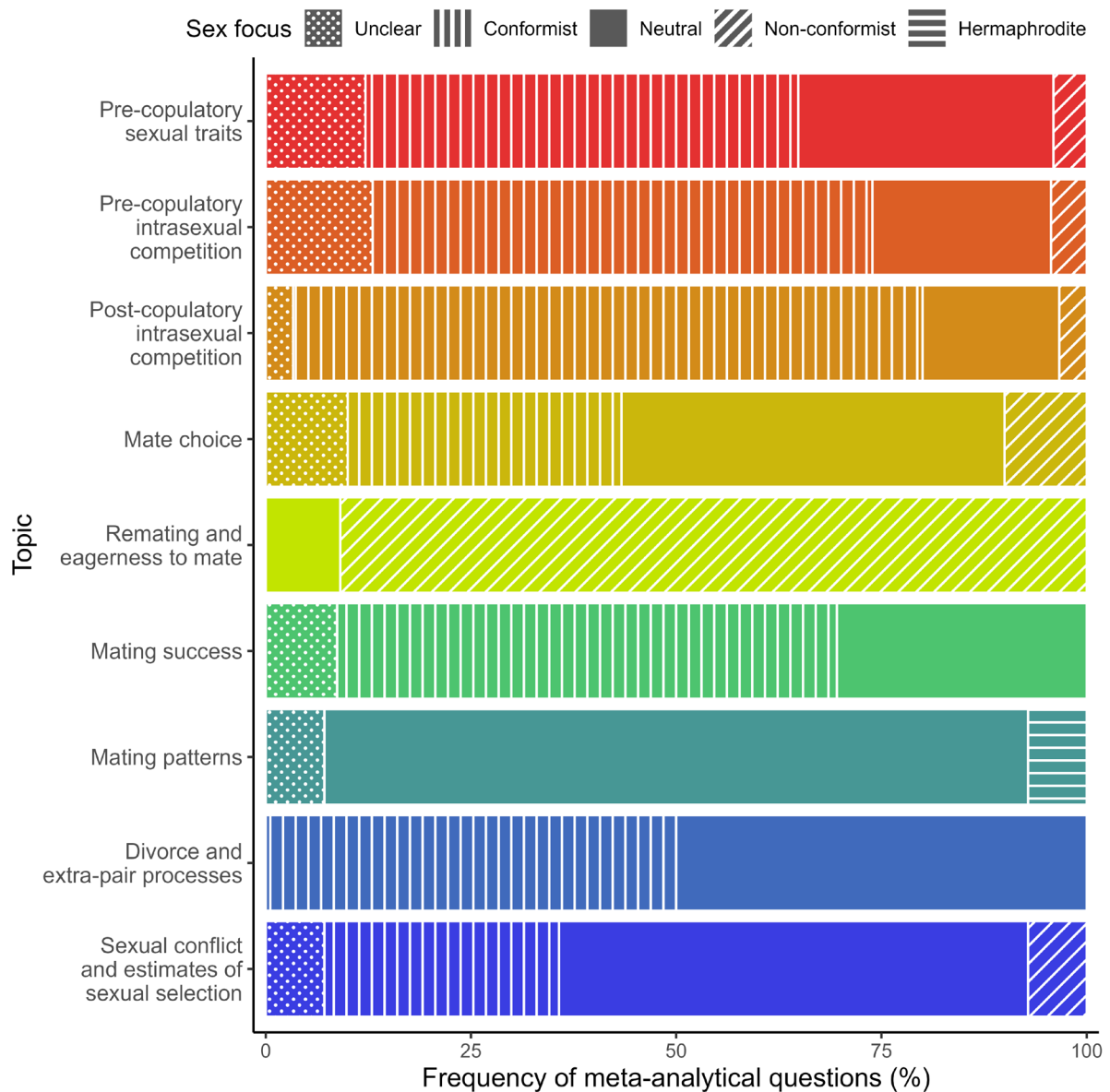
464 (heterosexual) social pairs or couples in copula. However, we emphasise that questions from  
465 other topics that are answered with sex-neutral data might still show a skewed ratio of males

466 and females in their dataset. For example, White (2020) evaluated whether structural colours  
467 are associated with individual quality in both sexes, but 146 effect sizes were from males and

468 only 29 were from females. This sex imbalance is quite common in other (not so) sex-neutral  
469 meta-analyses from our systematic map, confirming that sex bias is a reality in the field of

470 sexual selection (see also Tang-Martinez, 2016; Pollo & Kasumovic, 2022).

471



472

473 Figure 8. Focus of meta-analytical questions in relation to the sex of individuals used and the  
 474 topic explored (see details in-text). Conformist refers to exclusive focus on males, and non-  
 475 conformist refers to exclusive focus on females (except for mate choice, in which this  
 476 rationale is inverted). Neutral refers to both sexes being focused.

477

478 The fact that the research literature investigates certain reproductive behaviours  
 479 mostly in one sex potentially reflects and contributes to researchers' belief of sex  
 480 stereotypical perceptions in the animal kingdom (Pollo & Kasumovic, 2022; Ah-King, 2022).

481 Darwin (1859, 1871) started this process: at first, he defined sexual selection as an  
482 evolutionary pressure acting exclusively on males, and frequently employed sexual  
483 stereotypes in his work. Although since then researchers have advanced our knowledge and  
484 perceptions on both sexes, the need to reduce sex bias in the field of sexual selection remains  
485 dire (Pollo & Kasumovic, 2022; Ah-King, 2022). In particular, researchers have emphasised  
486 the importance of not neglecting females in the study of sexual selection and related topics  
487 (e.g. Gowaty, 1997; Hare & Simmons, 2019; Rosenthal & Ryan, 2022). For instance, even  
488 though post-copulatory processes may depend on females as much as on males, female  
489 genitalia and reproductive organs have been largely overlooked, highlighted by recent  
490 discoveries and definitions (e.g. Folwell *et al.*, 2022; Keeffe & Brennan, 2023). Furthermore,  
491 only two meta-analytical studies from our dataset presented questions exploring the  
492 interaction between female and male traits in this context: Joly & Schiffer (2010) evaluated  
493 whether (female) receptacle length is associated with sperm length, while Myers *et al.* (2020)  
494 assessed whether presence of ovarian fluid is associated with sperm motility. Thus, we urge  
495 researchers to consider their role in contributing to the construction of a truly sex-neutral  
496 literature in the field of sexual selection (see also Ahnesjö *et al.*, 2020).

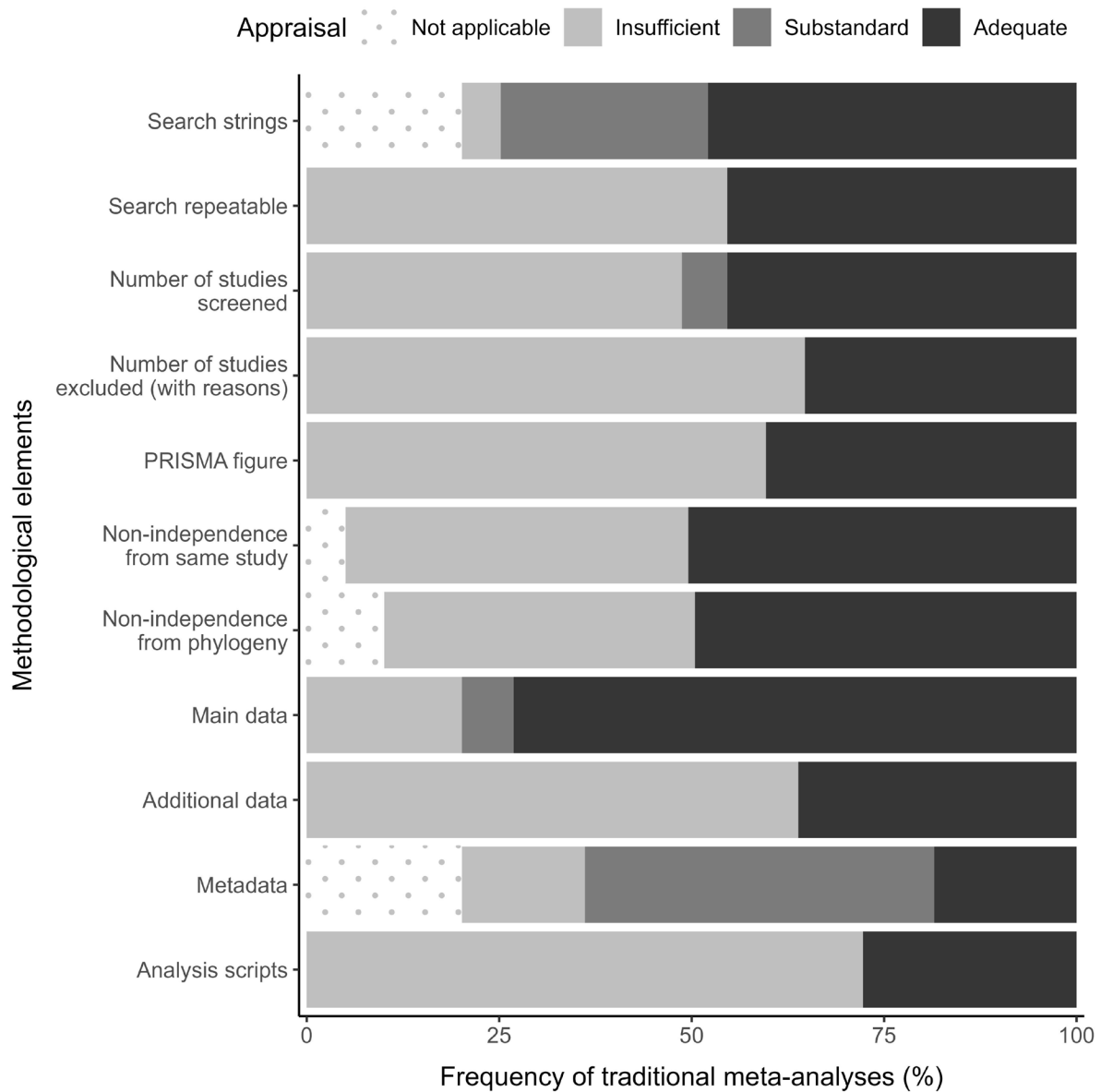
497

### 498 (3) Reporting appraisal of traditional meta-analyses

499 Almost 80% (n = 119) of the studies included in our systematic map (i.e. broad sense meta-  
500 analyses, see section II.2) were classified as traditional meta-analyses (i.e. used traditional  
501 effect sizes and properly modelled heterogeneity using additive weighting rather than  
502 multiplicative weighting; see Nakagawa *et al.* (2023a). Remaining studies (n = 33) used other  
503 comparative methods, from simple linear regressions on raw data (e.g. Bailey & Hammond,  
504 2003) to more sophisticated statistical approaches (e.g. Wang *et al.*, 2019 used formal effect  
505 sizes and mixed effects models with multiplicative weights where heterogeneity cannot be

506 easily obtained). In this section, we evaluated methodological details only from traditional  
 507 meta-analyses, as other comparative studies commonly do not adhere to classic meta-  
 508 analytical standards. Figures 9 and 10 summarise results of our appraisal, which are  
 509 comparable to other similar studies (e.g. Philibert, Loyce & Makowski, 2012; O’Leary *et al.*,  
 510 2016; O’Dea *et al.*, 2021; Nakagawa *et al.*, 2023b; Yang *et al.*, 2023a).

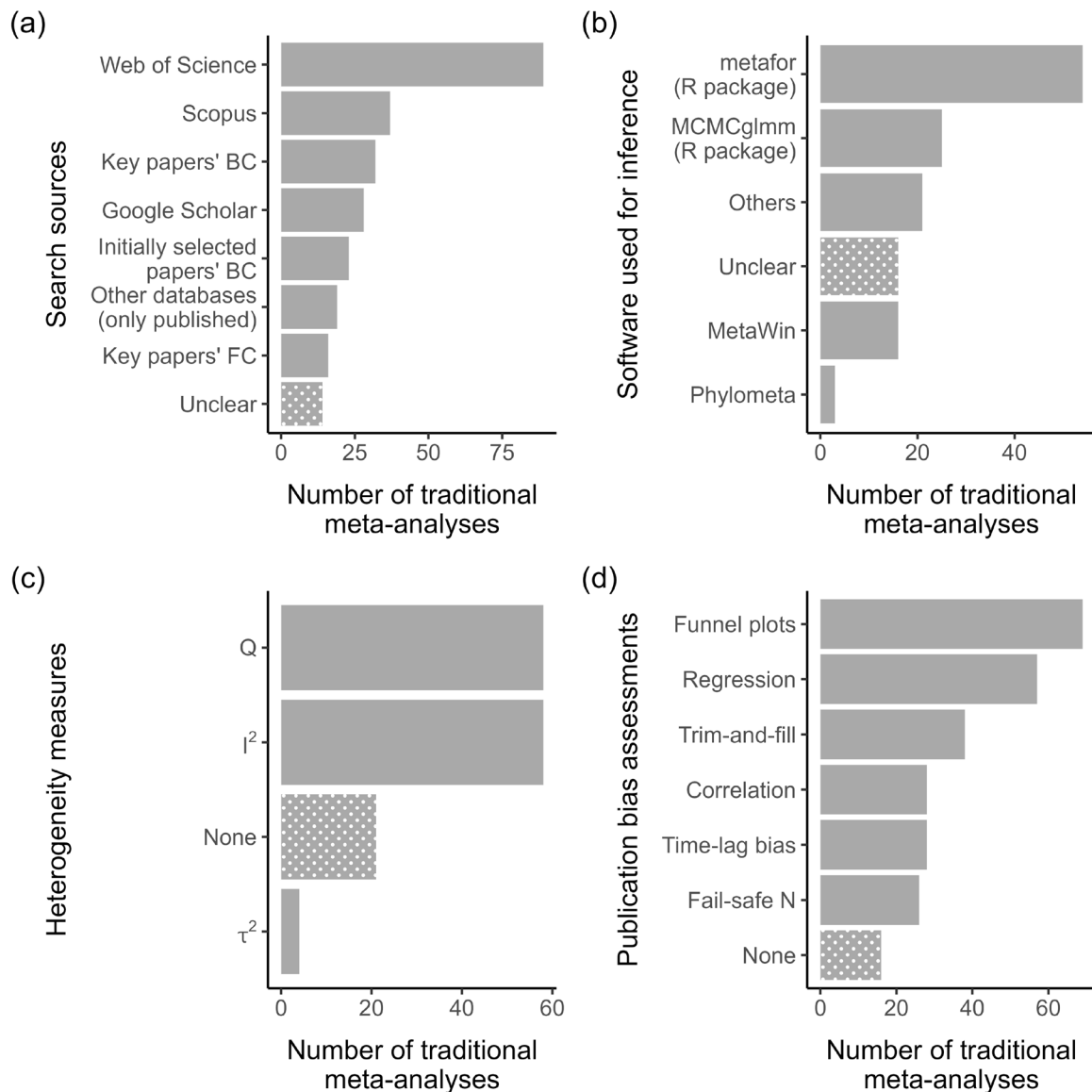
511



512

513 Figure 9. Appraisal of traditional meta-analyses on topics associated with sexual selection  
 514 regarding several methodological elements. Elements poorly provided or absent were

515 considered insufficient. Substandard appraisal was given to elements that were provided but  
 516 with caveats, while adequate appraisal was given to elements competently provided. Certain  
 517 elements were not applicable to be judged depending on the meta-analytical study (see details  
 518 on section III.3).  
 519



520  
 521 Figure 10. Details of methodological elements used by traditional meta-analyses on topics  
 522 associated with sexual selection. Note that each meta-analysis could utilise multiple search

523 sources (A), software (B), heterogeneity measures (C), and publication bias assessment tools  
524 (D). In the left top plot (A), ‘BC’ refers to backward citations and ‘FC’ to forward citations.

525

#### 526 (a) Searches

527 Meta-analyses should describe their search methods in detail to enable repeatability of the  
528 search process (i.e. retrieval of the same set of empirical studies). This first involves  
529 describing the exact sources used to conduct searches. We found that 88% of the traditional  
530 meta-analyses provided this information. In these meta-analyses, the most popular search  
531 sources were databases (e.g. Web of Science, Scopus), followed by backward citations (i.e.  
532 reference lists) from relevant key papers or initially selected studies (Figure 10A). These  
533 sources usually do not capture grey literature (i.e. unpublished studies). Sources that can  
534 capture grey literature (e.g. Google Scholar, BASE, etc) were rarely used in our sample of  
535 meta-analyses. Note that every meta-analytical study should use multiple search sources to be  
536 comprehensive: we found that 68% of traditional meta-analyses used at least two search  
537 sources.

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

547 We further assessed the repeatability of searches conducted in traditional meta-  
548 analyses, using the information we collected about search sources and queries (for which  
549 substandard string provision was not considered repeatable) coupled with other details. For  
550 instance, repeatable searches had to both specify when they were conducted (at least month  
551 and year) and their sources had to be accessible in 2023 (some older databases were no longer  
552 available). We found that traditional meta-analyses' searches from our dataset were  
553 repeatable in approximately 45% of the cases (Figure 9).

554

#### 555 (b) Screening process

556 Meta-analytical studies need to be transparent with their screening decisions, explicitly  
557 reporting the number of studies screened and the number of studies excluded at the full-text  
558 screening stage with justifications that clarify each of these exclusions. Thus, we first verified  
559 whether traditional meta-analyses provided the number of studies screened in at least two  
560 screening phases (i.e. initial and full-text). We considered the screening information provided  
561 to be insufficient when the number of studies screened were absent, and as substandard when  
562 this number was reported for only one phase or when it was not exact (e.g. Hasik &  
563 Siepielski, 2022). This resulted in 49%, 45%, and 6% of traditional meta-analyses from our  
564 systematic map showing insufficient, adequate, and substandard information on the number  
565 of studies screened, respectively (Figure 9).

566 We then verified details on screening decisions, in which we deemed as insufficient  
567 information when studies provided no information, only information for their initial screening  
568 phase (e.g. Nolzco *et al.*, 2022), or a list of exclusion reasons with the total number of  
569 excluded papers (instead of exclusion reason for each paper, e.g. Weaver *et al.*, 2018). This  
570 culminated in only 35% of traditional meta-analyses properly describing the justification for  
571 their full-text excluded papers (Figure 9).

572 Both the number of studies screened and excluded (with justifications) should ideally  
573 be presented in a PRISMA-like diagram, which summarises both the search and screening  
574 processes (O’Dea *et al.*, 2021). A few papers presented figures that lacked too many  
575 necessary diagram elements, so we considered them insufficient (e.g. Harts, Booksmythe &  
576 Jennions, 2016; Hasik & Siepielski, 2022). We found that only 40% of the traditional meta-  
577 analyses from our dataset showed adequate PRISMA-like diagrams (Figure 9).

578

#### 579 (c) Software and data non-independence

580 Non-independence among effect sizes often occurs in meta-analyses, which can lead to false  
581 conclusions if not properly addressed (Noble *et al.*, 2017; Cinar, Nakagawa & Viechtbauer,  
582 2022). We specifically examined whether traditional meta-analyses from our dataset dealt  
583 with non-independence from shared study identities (i.e. when at least two effect sizes are  
584 extracted from the same study) and from phylogenetic relatedness. We found that  
585 approximately half of the meta-analytical studies evaluated dealt with at least one of these  
586 non-independence sources (Figure 9), usually through random factors in meta-analytical  
587 models. We emphasise that non-independence might be entirely absent (i.e. not applicable;  
588 Figure 9) from meta-analyses whose effect sizes are all extracted from different studies (i.e.  
589 independent) or when they investigate only a single species (see section III.2.a). Related to  
590 this, most meta-analyses were conducted using the R packages *metafor* (Viechtbauer, 2010)  
591 and/or *MCMCglmm* (Hadfield, 2010) (Figure 10B). These packages are the most appropriate  
592 meta-analytical tools as they can incorporate phylogeny and other types of non-independence.

593

#### 594 (d) Analytical reproducibility and transparency

595 We evaluated whether meta-analyses transparently provided the main components needed for  
596 analytical reproducibility: sharing of the main data, metadata, additional data, software



597 information, and analysis scripts. Lack of data transparency is a major obstacle for  
598 reproducibility (Wilkinson *et al.*, 2016; Munafò *et al.*, 2017). First, meta-analyses need to  
599 provide data with effect size values and all other variables used in their analyses (e.g.  
600 moderators). We refer to these datasets as main data, as studies can also provide additional  
601 data (e.g. raw measurements or location from which they were extracted in empirical papers).  
602 We found that 73% and 7% of traditional meta-analyses on topics related to sexual selection  
603 provided all or some (i.e. substandard) of their main data, respectively (Figure 9). These  
604 findings are a little more optimistic than those found by a survey of the primary literature in  
605 ecology and evolution (Roche *et al.*, 2015). However, we note that many datasets were  
606 simply provided in a form of tables in-text (rather than separate data files), which is  
607 considered as a suboptimal practice. In addition, data were supposedly provided but could not  
608 be accessed in some cases (e.g. due to broken links; Guindre-Parker & Love, 2014;  
609 Dougherty, 2023), emphasising that authors must ensure that any resources mentioned in  
610 their papers are truly available to readers. Despite main data being shared in most meta-  
611 analytical studies, only 36% of meta-analyses evaluated provided additional relevant data  
612 (Figure 9), highlighting another obstacle for reproducibility.

613         To enhance reproducibility, data should ideally be provided with a separate metadata  
614 file (i.e. information that fully describes all fields from the main dataset provided). Metadata  
615 were provided in only 18% of traditional meta-analyses (Figure 9). Nonetheless, another 45%  
616 of the studies showed easily understandable data (e.g. from the study context, no acronyms  
617 used) and, even though we considered these cases as substandard for lacking proper metadata  
618 (Figure 9), these resources were occasionally clear and informative (e.g. tables in Meunier *et*  
619 *al.*, 2011; Graham *et al.*, 2015). We also note that metadata were not applicable for traditional  
620 meta-analyses that did not provide any of their main data (ca. 20%).

621 At last, sharing analysis scripts is essential for others to reproduce meta-analytical  
622 findings (Piccolo & Frampton, 2016; Culina *et al.*, 2020). We found that only 28% of the  
623 studies evaluated in our appraisal appropriately shared their code (Figure 9). The remaining  
624 72% either used point-and-click software (n = 27; e.g. MetaWin, Phylometa, etc; Figure  
625 10B), did not mention the software used (n = 16; although some papers might have not used  
626 any, e.g. manual calculations), or simply provided no code despite using other software (n =  
627 43). Our finding is similar to recent reports on code availability in ecology (Culina *et al.*,  
628 2020). The low code sharing can be a result of lack of incentives for authors to share their  
629 code (see Gomes *et al.*, 2022) or lack of the awareness of the importance of software in  
630 research.

631

#### 632 (e) Heterogeneity and publication bias

633 Heterogeneity measures the amount of variation among effect sizes, thus being critical to  
634 understanding the generality of overall effect sizes shown in meta-analytical studies (Spake *et*  
635 *al.*, 2022); see section III.6). We found that 82% of traditional meta-analyses calculated at  
636 least one heterogeneity measure. Those that did most frequently used  $Q$  and/or  $I^2$  (Figure  
637 10C). We note that  $H^2$  (Lynch, 1991) or Pagel's  $\lambda$  were commonly present in phylogenetic  
638 regressions, which we did not consider proper stand-alone heterogeneity measures for a meta-  
639 analysis.

640 Meta-analytical studies also must investigate publication bias in their included  
641 dataset, as this can drastically impact results' magnitude and sign errors (Yang *et al.*, 2023b).  
642 87% of traditional meta-analyses from our dataset assessed publication bias in some way.  
643 Funnel plots were the most popular tool to address publication bias (Figure 10D), similar to  
644 Nakagawa *et al.* (2021)'s findings.

645

646 (f) Other elements

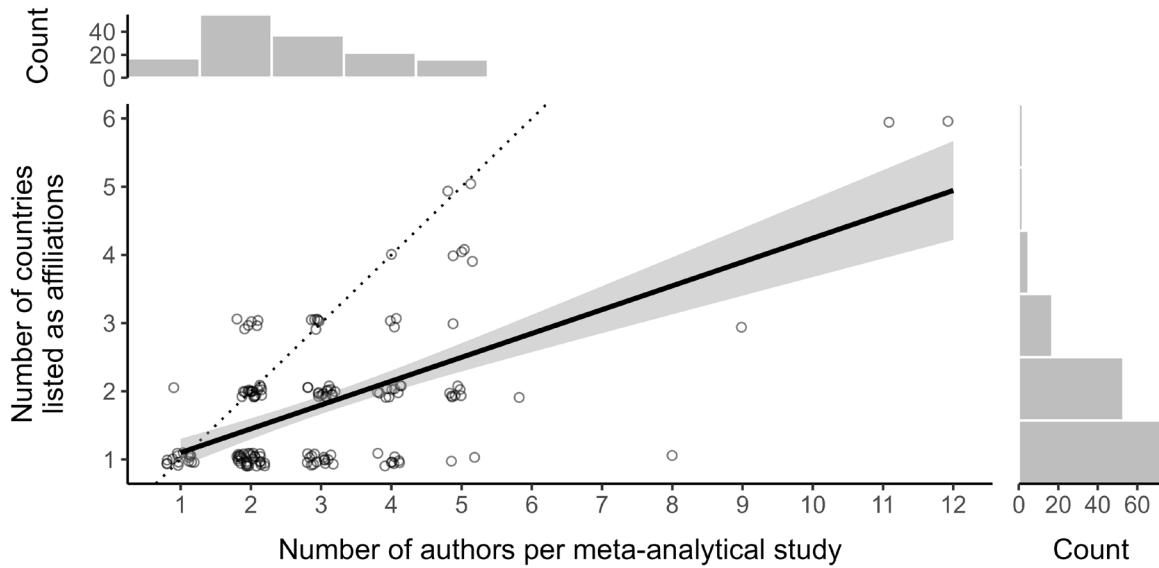
647 We verified the occurrence of several other important methodological elements in traditional  
648 meta-analyses, but rarely found them. For instance, only one study was pre-registered (e.g.  
649 Kim *et al.*, 2021) and none mentioned post-hoc hypotheses (although there were cases of  
650 post-hoc analyses; e.g. Winternitz *et al.*, 2017; Parker *et al.*, 2018; Kim *et al.*, 2021). In  
651 addition, the quality of empirical data was evaluated in only four traditional meta-analyses:  
652 Simons & Verhulst (2011) and Parker *et al.* (2018) examined empirical pseudoreplication,  
653 Kim *et al.* (2021) intended to verify the effect of blind data collection (but ironically found  
654 that no empirical papers collected data blindly), and Culina, Radersma & Sheldon (2015)  
655 evaluated the trustworthiness of empirical studies from which they extracted data. This near  
656 absence of quality assessment of primary studies has also been detected in ecological  
657 systematic reviews despite being imperative to reduce bias (Stanhope & Weinstein, 2022).  
658 However, we emphasise that here we only considered generic quality assessments (i.e. that  
659 are relevant for all types of studies), but that there are also more specific assessments (e.g. via  
660 experiment design; (Davies, Lewis & Dougherty, 2020; Pollo, Nakagawa & Kasumovic,  
661 2022).

662

663 *(4) Bibliometric analysis*

664 The 152 meta-analyses included in our study were authored by 326 different authors  
665 affiliated to institutions from 31 countries (Figure 11; Figure 12). The median for the number  
666 of authors per study was three ( $\bar{x} = 2.97$ , 95% CI = 2.71 to 3.24), while the median of the  
667 number of countries per study was two ( $\bar{x} = 1.79$ , 95% CI = 1.63 to 1.95) (Figure 11).  
668 Intuitively, the number of different countries from authors' affiliations increased with the  
669 number of authors (Figure 11). We present more results from our bibliometric analysis in the  
670 subsections below, but we discuss the impacts of all these findings in section III.6.d.

671



672

673 Figure 11. Relationship between number of authors for each meta-analytical study and  
674 number of countries listed as affiliations. The dotted line highlights a perfect correlation  
675 between these two variables, while the continuous line represents the best fit from a linear  
676 regression. Histograms on top and on the right indicate the number of studies for each  
677 number of authors and countries listed as affiliations, respectively.

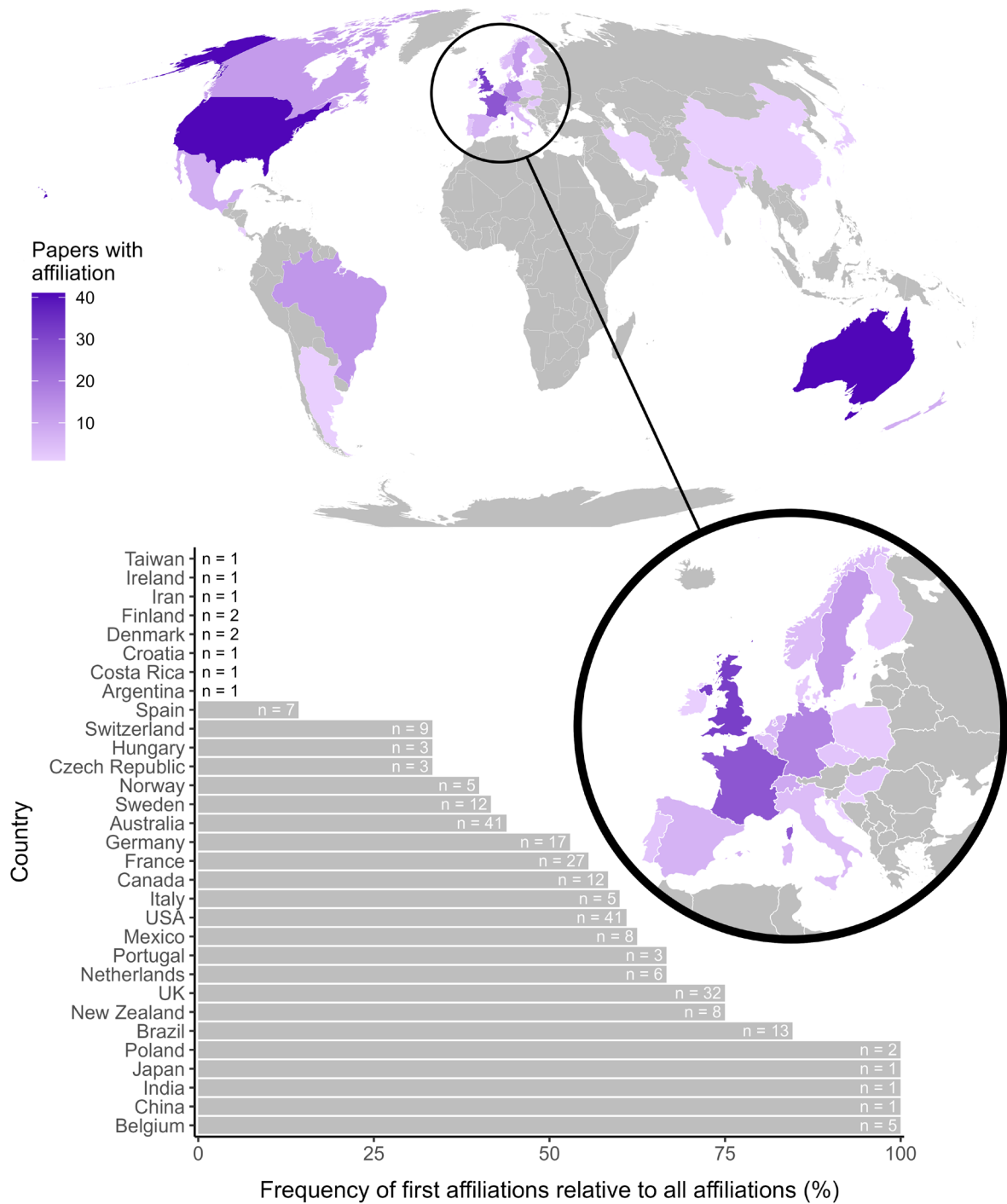
678

679 (a) Authors' affiliations

680 Australia and the United States of America (hereby USA) were the most prolific countries in  
681 publishing meta-analyses on topics associated with sexual selection, each with 41 meta-  
682 analyses being authored by at least one researcher affiliated to an institution located there  
683 (Figure 12). We detected only a few developing countries (i.e. Global South) as affiliations in  
684 the evaluated meta-analyses. In fact, the only countries with more than a single study  
685 affiliated outside of Anglo-America, Europe, or Oceania, were Brazil and Mexico (Figure  
686 12).

687           The first affiliation listed in each study, which is usually associated with the lead  
688 authorship, revealed a similar authorship pattern. The USA also led with the highest number  
689 (n = 25) of studies with one of its institutions as the first affiliation listed in papers, albeit the  
690 United Kingdom followed close behind with 24 first affiliations. The proportion of first  
691 affiliations to all affiliations seen per country can serve as a proxy of how dependent a  
692 country is on international collaborations (Figure 12). For example, despite seven meta-  
693 analytical studies being associated with an institution from Spain, only in one of them a  
694 Spanish institution was the first affiliation listed. In contrast, Belgian institutions were first  
695 listed as affiliations in all of five meta-analyses associated with Belgium. We emphasise,  
696 however, that this proportion tends to extreme values (i.e. none or all) with fewer studies  
697 associated with a country (Figure 12). Furthermore, we note that almost half of all meta-  
698 analyses evaluated (n = 73) were affiliated to a single country (Figure 12).

699



700

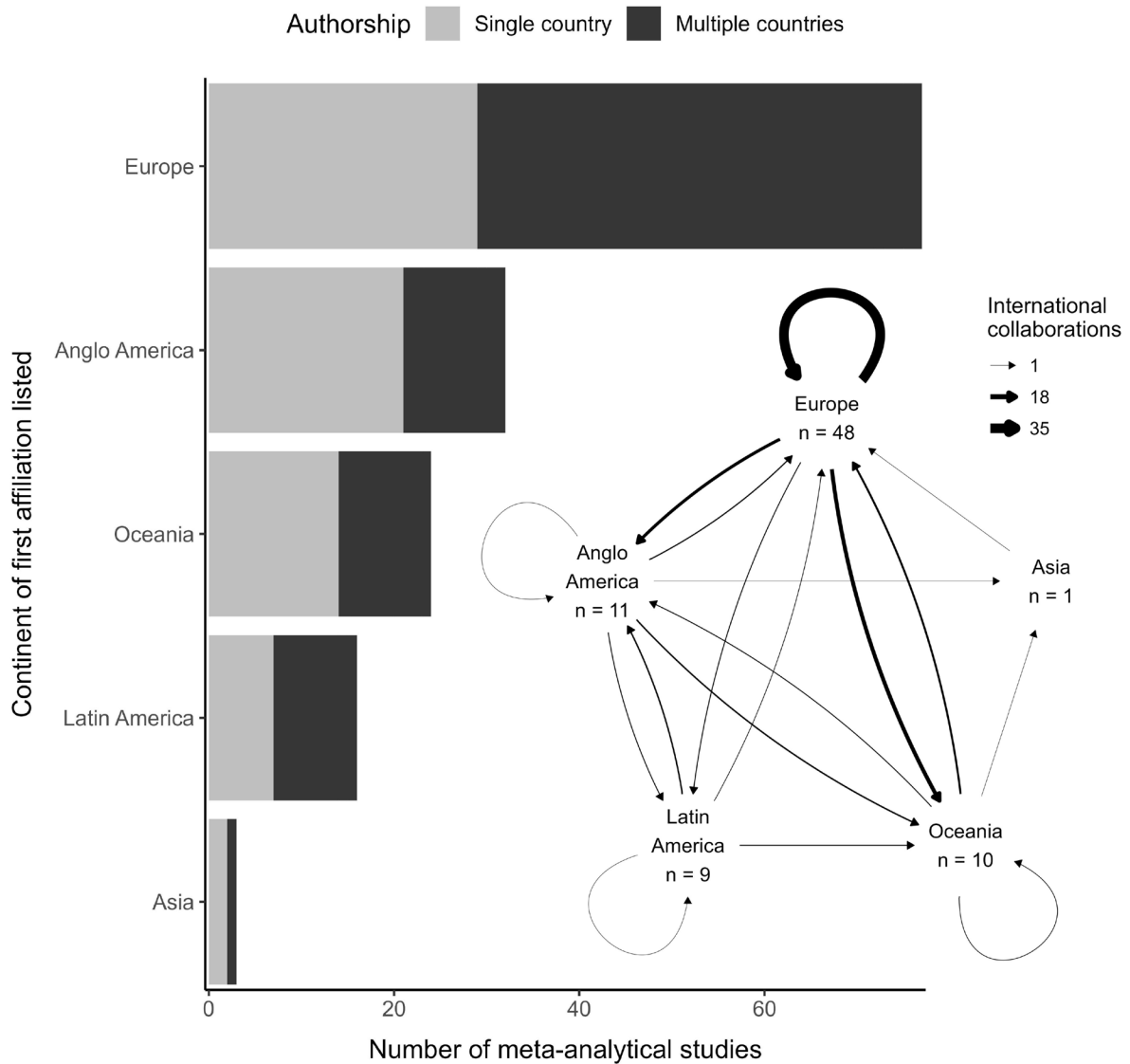
701 Figure 12. Affiliations reported in meta-analytical studies on topics associated with sexual  
 702 selection. Colour intensity in maps (top and inset) illustrate the number of papers in which  
 703 countries' institutions were recorded as authors' affiliations, greyed countries representing  
 704 zero. Bar plot (bottom) shows the percentage of affiliations that were reported first in papers

705 (i.e. affiliation of first author) per country, with the total number of affiliations per country  
706 given inside each bar.

707

708           Shifting the focus to continents, we observed that approximately half ( $n = 77$ ) of all  
709 first affiliations belong to Europe (Figures 12 and 13). Papers with first affiliations located in  
710 Europe were also more likely to be associated with institutions from multiple countries (and  
711 thus have international collaborations) compared to papers with other continents as first  
712 affiliation (Figure 13). However, most of these international collaborations were between  
713 countries in the same continent (Figure 13). For example, out of 48 meta-analyses that  
714 originated in Europe with multiple countries affiliated to them, 35 had at least one  
715 international collaboration with another European institution, while no author from another  
716 continent was involved in 25 of them.

717



718

719 Figure 13. Collaborations on a continental level. The barplot shows the number of meta-

720 analytical studies per continent that listed affiliations from either one or multiple countries.

721 The network shows the number of papers that contain affiliations from multiple countries

722 (same as darker bars in the barplot) per continent, with arrows representing international

723 collaborations (from continent of the first affiliation to the continent of posterior affiliations).

724

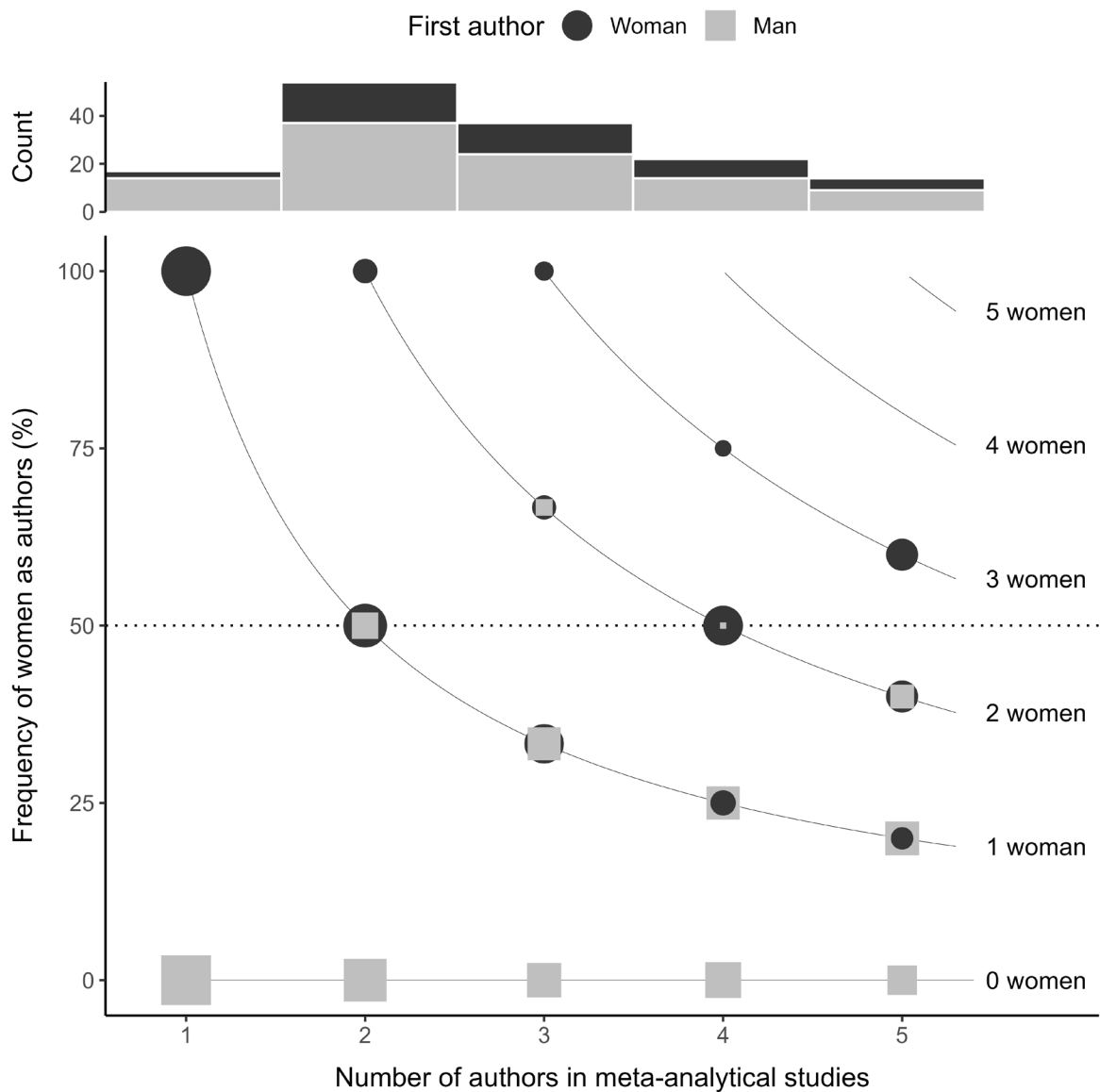
725 (b) Authors' gender

726 We found gender bias in authors of meta-analyses on topics related to sexual selection

727 (Figure 14): only 37% of these authors were classified as women (n = 119), opposed to 61%



728 classified as men (n = 199; gender could not be assigned to the remaining 2% of authors).  
 729 This gender disparity increased when considering only first authors, as 68% of them were  
 730 identified as men and 31% as women (1% was unknown). The number of women in multi-  
 731 authored studies was rarely greater than the number of men, even when women were first  
 732 authors (Figure 14). On the other hand, men predominated in research projects led by them.  
 733 In fact, we detected only three studies led by men with a greater number of women than men  
 734 as participating authors (Figure 14).  
 735



736

737 Figure 14. Authorship by gender and number of authors in meta-analytical studies on topics  
738 related to sexual selection. Shape size represents the proportion of studies observed for each  
739 number of authors and for each first author's gender. Four meta-analytical studies with more  
740 than five authors and another four that contained a name that could not be assigned to a  
741 binary gender are not shown.

742

743 *(5) Details and in-depth discussion regarding topics related to sexual selection*

744 In this section, we discuss the study questions (and the research topics they belonged to) that  
745 we extracted from meta-analyses related to sexual selection (see section III.2.e, Figure 7). We  
746 found that the most popular topic was pre-copulatory sexual traits (74 questions from 59  
747 meta-analyses), followed by mate choice and post-copulatory intrasexual competition (30  
748 questions each, from 29 and 27 meta-analyses, respectively). To improve readability, we  
749 limited citing relevant studies related to patterns we described to five citations. In cases in  
750 which more than five meta-analytical studies were relevant and should be cited, we instead  
751 refer to the Supplementary material to encourage readers to check all questions fully  
752 described there. In addition, to avoid repetition, questions that did fit into multiple topics  
753 were occasionally omitted from relevant subsections if they had already been mentioned.

754

755 (a) Pre-copulatory sexual traits

756 In this category of our classification framework, we included questions explicitly mentioning  
757 pre-copulatory sexual traits, such as secondary sexual characteristics, ornaments, courtship,  
758 and sexual signals. Although weapons would technically fit here (see section III.6.b), we  
759 noticed that a distinct set of meta-analyses focused on them, so we classified them differently  
760 (see section III.5.b). However, we note that some meta-analyses discussed in the current  
761 section grouped several different traits under a single label (e.g. secondary sexual traits), and

762 weapons might be inadvertently amongst them. In total, this category encompassed 74  
763 questions from 59 meta-analytical studies, revealing this topic as the most popular in the  
764 meta-analytical literature related to sexual selection (Figure 7).

765         The emphasis on pre-copulatory sexual traits is expected, as Darwin (1871) himself  
766 used them to develop the theory of sexual selection (see section III.6.b). He proposed that  
767 ornaments and sexual signals evolved via mate choice, an idea that was rejected by his peers  
768 at the time (Hoquet & Lewandowsky, 2015). Nonetheless, the literature on ornaments and  
769 sexual signals later flourished when a debate among evolutionary biologists was established:  
770 whether these traits and signals evolved because they reflect greater genetic quality to  
771 prospective mates (“good genes” model and its “handicap principle” extension; Zahavi, 1975,  
772 1977) or simply because they genetically correlate with mate preference for themselves (i.e.  
773 Fisherian runaway process; Fisher, 1930; see also Eshel, Volovik & Sansone, 2000; Kokko,  
774 2001; Hoquet & Lewandowsky, 2015). Possibly because the latter is complex and difficult to  
775 measure (but see Greenfield *et al.*, 2014), the former has received much more empirical  
776 attention.

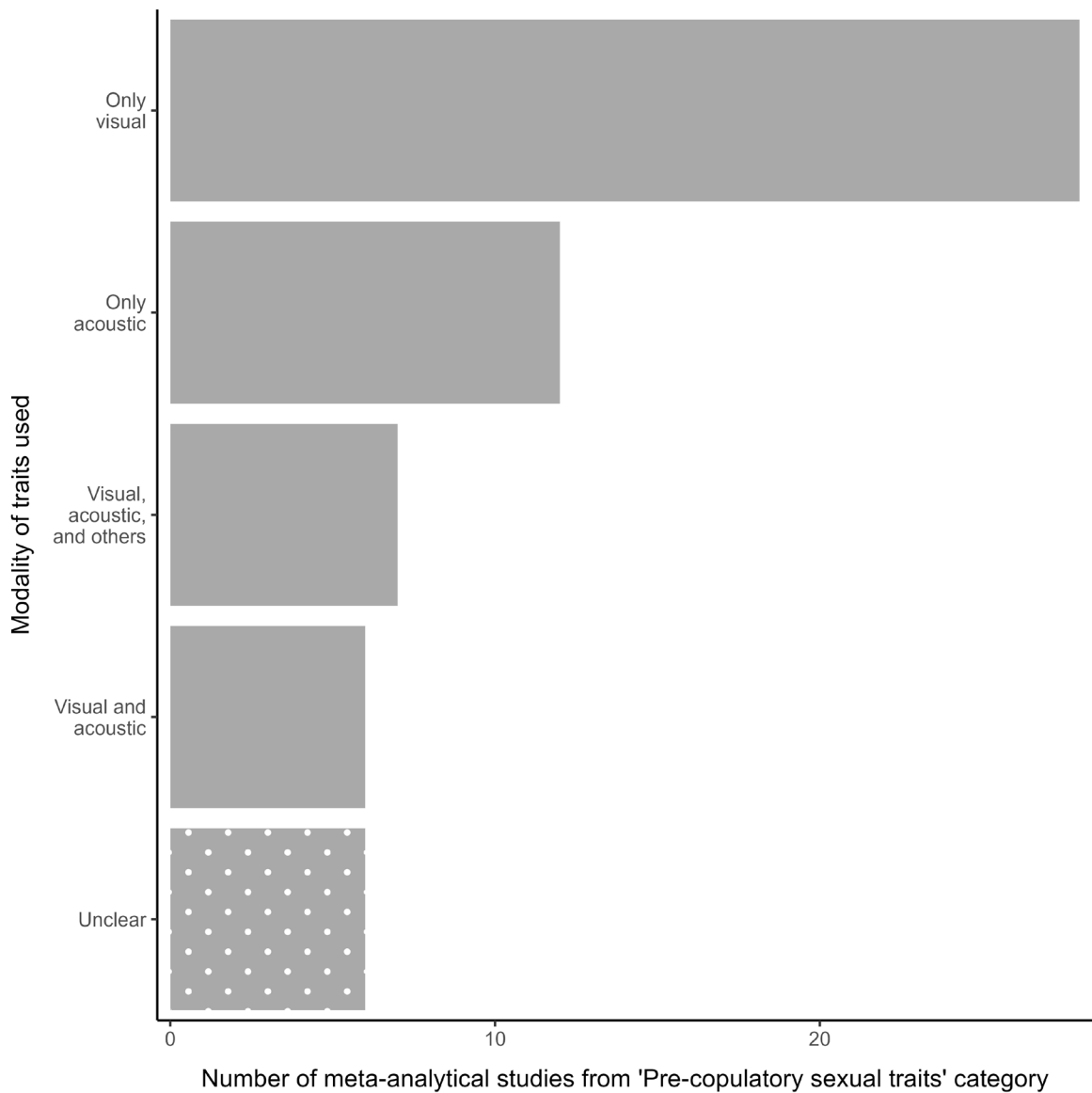
777         On one hand, some proponents of the good genes model (e.g. Andersson, 1994)  
778 predicted that ornaments and sexual signals would be linked to fitness-impacting measures  
779 (e.g. survival, fecundity, viability, overall reproductive success; see Kokko, 2001), which was  
780 tested by many different meta-analyses (Table S5). On the other hand, Grafen (1990a, 1990b)  
781 popularised Zahavi’s (1975, 1977) idea that ornaments and sexual signals must be condition-  
782 dependent to be honest (reviewed and contested in Penn & Számadó, 2020; see also Getty,  
783 2006), shifting the attention of the research community to more direct questions. It is  
784 unsurprising then that 26 meta-analyses in our systematic map contain at least one question  
785 asking whether the expression of ornaments and sexual signals are related to the expression  
786 of other traits (e.g. age, body size) or to proxies of individual quality (e.g. parasite load; or

787 their manipulation, e.g. diet supplementation, stress) (Table S5). Questions of this nature do  
788 not aim to test whether pre-copulatory sexual traits are indeed under sexual selection, but  
789 simply whether they function as reliable cues of good genes to prospective mates.

790         Conversely, a variety of meta-analytical studies ( $n = 18$ ) tested whether certain  
791 ornaments and sexual signals might be in fact under selection by verifying their relationship  
792 with intrasexual competition (e.g. dominance rank or aggression; Nakagawa *et al.*, 2007;  
793 Yasukawa *et al.*, 2010; Santos, Scheck & Nakagawa, 2011; Parker, 2013; Sánchez-Tójar *et*  
794 *al.*, 2018), species recognition (Ord & Stamps, 2009; Ord, King & Young, 2011; Parker *et*  
795 *al.*, 2018), attractiveness in mate choice experiments (Parker & Ligon, 2003; Simons &  
796 Verhulst, 2011; Hernández *et al.*, 2021), mating success, or extra-pair patterns (see in Table  
797 S5). Other meta-analytical studies explored whether courtship behaviours, ornaments, and/or  
798 sexual signals are related to specific biotic (e.g. density, predation, etc; Weir, Grant &  
799 Hutchings, 2011; De Jong *et al.*, 2012; Dougherty, 2021a; White, Latty & Umbers, 2022) and  
800 abiotic conditions (e.g. habitat structure, band colouration, etc; Boncoraglio & Saino, 2007;  
801 Seguin & Forstmeier, 2012; Parris & McCarthy, 2013). At last, other specific meta-analytic  
802 studies assessed sexual traits' additive genetic variation (Pomiankowski & Møller, 1995) and  
803 heritability (Prokop *et al.*, 2012; Prokuda & Roff, 2014), compared the allometry of sexual  
804 traits depending on their function and denomination (Voje, 2016; Rodríguez & Eberhard,  
805 2019), verified whether pre-copulatory sexual traits are associated with sperm quality (Mautz,  
806 Møller & Jennions, 2013), examined the interplay between call length and reply latency  
807 across species (Bailey & Hammond, 2003), and evaluated the association between expression  
808 of possibly sexually selected traits and speciation rates (Kraaijeveld, Kraaijeveld-Smit &  
809 Maan, 2011).

810         We found that most questions related to pre-copulatory sexual traits from meta-  
811 analyses explored only visual and/or acoustic characteristics (Figure 15; Table S6). In

812 addition, some studies were unclear on the exact traits used (see also section III.6.b). We  
813 observed only seven meta-analytical studies with a question focusing on pre-copulatory  
814 sexual traits from other modalities (Figure 15; Table S6). Yet, even in these studies, visual  
815 and acoustic traits predominate over others, revealing that some sensory modalities (e.g.  
816 olfactory) are neglected. We discuss the implications of this pattern in section III.6.b.  
817



818

819 Figure 15. Sensory modality of traits nominated as secondary sexual characteristics,  
820 ornaments, or sexual signals from meta-analyses with at least one question categorised as  
821 “Pre-copulatory sexual traits”. Visual traits include colour, morphology, and visual displays.

822

### 823 (b) Pre-copulatory intrasexual competition and associated traits

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

833         Animal weapons represent the heartthrob of intrasexual competition as these traits are  
834 pivotal for intrasexual combat as well as for assessment signalling to avoid physical  
835 confrontations in many species (Emlen, 2008; Rico-Guevara & Hurme, 2019). A couple of  
836 meta-analyses tested a key assumption related to these traits: whether weapons are indeed  
837 related to contest success (Vieira & Peixoto, 2013; Palaoro & Peixoto, 2022; although the  
838 first used resource holding potential, which included other traits). Similarly, Kelly (2008)  
839 examined the relationship between resource holding potential (considering weapons and other  
840 traits), resource value, and reproductive success. Furthermore, some authors explored  
841 whether expression of weaponry is associated with certain contexts, such as the type of  
842 disputed resource (e.g. mates vs. territory; Maciel, Oliveira & Peixoto, 2023) or the  
843 availability of reproductive sites (Alissa, 2018). Moreover, Menezes & Palaoro (2022)

844 investigated whether size and number of spurs are associated with body and wing size, which  
845 are traits connected to flight capacity. Lastly, Lüpold *et al.* (2015) verified whether the  
846 expression of weapons is linked to sperm length, whereas Rodríguez & Eberhard (2019)  
847 compared allometry slopes of weapons with those of ornaments.

848 As previously mentioned, some studies evaluated whether ornaments are linked to  
849 aggression or dominance (Nakagawa *et al.*, 2007; Yasukawa *et al.*, 2010; Santos *et al.*, 2011;  
850 Parker, 2013; Sánchez-Tójar *et al.*, 2018). In respect to territoriality, Ord (2021) assessed the  
851 costs associated with this behaviour whilst (Ord *et al.*, 2011) verified whether species  
852 recognition occurs for territorial signals. Other meta-analytical investigations explored  
853 whether different contexts and conditions are associated with the expression and intensity of  
854 intrasexual competition, such as operational sex ratio (Weir *et al.*, 2011), environmental  
855 stability (Peixoto, Medina & Mendoza-Cuenca, 2014), and availability of reproductive sites  
856 (Alissa, 2018). Finally, certain meta-analyses attempted to answer questions involving other  
857 topics by examining the following relationships: mating success and fighting frequency  
858 (Fiske, Rintamaki & Karvonen, 1998) or social dominance (Majolo *et al.*, 2012), strength of  
859 mate choice and traits determinant to intrasexual competition success or attractiveness (Pollo  
860 *et al.*, 2022), and mate monopolisation and estimates of sexual selection (Macedo-Rego *et al.*,  
861 2020b) or the effect of body size on reproductive success (Macedo-Rego *et al.*, 2020c).

862

### 863 (c) Post-copulatory intrasexual competition and associated traits

864 Post-copulatory intrasexual competition, popularly known as sperm competition, occurs  
865 when ejaculates from different males compete for a set of ova (Parker, 1970; Parker &  
866 Pizzari, 2010). Darwin (1871) did not know this was possible, so this subject emerged much  
867 later than pre-copulatory processes in the literature of sexual selection. In this category, we  
868 gathered 30 meta-analytical questions (from 27 studies) involving gamete traits, ejaculate

869 traits, primary sexual characteristics (i.e. traits necessary for reproduction, e.g. gonads and  
870 genitalia, see section III.6.b), risk and intensity of sperm competition, as well as paternity  
871 protection behaviours (e.g. mate guarding) (Figure 7).

872 Most questions in this category concentrated on the expression of gametes, ejaculates,  
873 and/or primary sexual traits. For example, several meta-analyses investigated the relationship  
874 between these traits, their allocation, or their production, and either (1) another type of trait  
875 (e.g. alternative reproductive tactics: Aguiar Del Matto, 2018; Dougherty *et al.*, 2022; body  
876 size or mass: Hayward & Gillooly, 2011; Lüpold & Fitzpatrick, 2015; Kim *et al.*, 2021;  
877 mating status: Zhang *et al.*, 2016; secondary sexual traits: Mautz *et al.*, 2013; weapons:  
878 Lüpold *et al.*, 2015), (2) a specific context (e.g. contaminants: Marmol, 2022; diet or nutrient  
879 intake: Crean & Senior, 2019; Macartney *et al.*, 2019; inbreeding: Losdat, Chang & Reid,  
880 2014; masculinization: Senior, Johnson & Nakagawa, 2016b; mate quality: Kelly & Jennions,  
881 2011; presence of ovarian fluid: Myers *et al.*, 2020; presence of rivals: delBarco-Trillo, 2011;  
882 Kelly & Jennions, 2011; sexual cannibalism: Dharmarathne & Herberstein, 2022;  
883 temperature: García-Roa *et al.*, 2020), or (3) a potential consequence (e.g. allometry patterns:  
884 Voje, 2016; patterns of sperm competition risk: Lüpold *et al.*, 2020; trait selection: Dougherty  
885 & Shuker, 2016; speciation rates: Kraaijeveld *et al.*, 2011). In addition, some studies  
886 evaluated the relationship between two gamete traits (e.g. Bernasconi & Hellriegel, 2005) or  
887 between a gamete trait and a primary sexual trait (especially gonad mass; e.g. Joly &  
888 Schiffer, 2010; Lüpold & Fitzpatrick, 2015; Lüpold *et al.*, 2015). The remaining questions  
889 that fit this category explored the connection between mate guarding and operational sex ratio  
890 (Weir *et al.*, 2011), individual quality, or paternity (Harts *et al.*, 2016); copula duration and  
891 sperm transfer (Dharmarathne & Herberstein, 2022) or operational sex ratio (Weir *et al.*,  
892 2011); and diverse measures of sperm competition and availability of reproductive sites  
893 (Alissa, 2018).



894

895 (d) Mate choice

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

914         Despite the many ways organisms can express mate preferences, assessing mate  
915 choice represents a challenge as decisions of individuals of both sexes are often involved  
916 (reviewed in Dougherty, 2020). Consider the outcome of an experiment in which a male and  
917 a female are put together in a confined space: if they copulate, was it a product of choice or  
918 coercion? If they do not, who was responsible for the rejection? The male, the female, or

919 both? As if the confusion from this simple scenario is not concerning enough, several meta-  
920 analytical studies combine mate choice experiment outcomes with observations from the field  
921 or of mixed groups of individuals regarding individuals' mating success (e.g. Møller &  
922 Thornhill, 1998; McLean, Bishop & Nakagawa, 2012; Kamiya *et al.*, 2014; Dougherty, 2023)  
923 or mating patterns (e.g. Yukilevich, 2012; Ihle & Forstmeier, 2013; Winternitz *et al.*, 2017;  
924 Rometsch, Torres-Dowdall & Meyer, 2020), which can be a product of other processes  
925 besides mate choice (see sections III.5.f and III.5.g).

926         Most questions that fit this category are simply concerned with identifying which  
927 aspects or traits are preferred by mates (Table S5). In contrast, other studies attempt to  
928 understand the conditions that modulate the strength and/or direction of mate choice  
929 expression (e.g. choosers' traits: Pollo *et al.*, 2022; Dougherty, 2023; Richardson & Zuk,  
930 2023; experimental design: Dougherty & Shuker, 2015; conspecifics' choices: Jones &  
931 DuVal, 2019; Davies *et al.*, 2020; temperature: Pilakouta & Baillet, 2022; various:  
932 Dougherty, 2021b). Although we note that species or population recognition might be a  
933 distinct process to mate choice (Rosenthal, 2017), five meta-analyses we included here  
934 explored whether individuals prefer conspecifics over others from different populations or  
935 species (Ord & Stamps, 2009; Ord *et al.*, 2011; Yukilevich, 2012; Parker *et al.*, 2018;  
936 Rometsch *et al.*, 2020). Lastly, other meta-analyses in this category evaluated the heritability  
937 of mate preferences (Prokuda & Roff, 2014) and the covariance between mate choice and  
938 preferred traits (Greenfield *et al.*, 2014).

939

#### 940 (e) Remating and eagerness to mate

941 In this category, we combined other reproductive aspects that have not yet been covered in  
942 the topics already discussed above: remating and eagerness to mate. While these are thought  
943 as simple cogs in the reproduction machine and not as mechanisms of sexual selection, they

944 can still be crucial to sexual selection. For example, when females of species with internal  
945 fertilisation mate more than once (i.e. are polyandrous), male-male competition may also  
946 occur post-copula through sperm competition, affecting sexual selection on males (Parker &  
947 Pizzari, 2010; Kvarnemo & Simmons, 2013). Despite the importance of examining factors  
948 related to remating and eagerness to mate, we detected only 11 questions (each from a  
949 different meta-analysis) that fitted this category (Figure 7).

950         The majority of the questions from this topic are alike: they evaluate the benefits  
951 and/or costs to individuals (or to their offspring) of mating multiple times versus mating once  
952 or fewer times (Table S5). Similarly, two other studies verified whether individuals' mating  
953 history can influence the available resources they have for further copulas, as well as their  
954 subsequent impact on the reproductive success of individuals they copulate with (Torres-Vila  
955 & Jennions, 2005; Zhang *et al.*, 2016), which ultimately could influence remating decisions.  
956 The remaining studies in this category are slightly distinct: Mori & Evenden (2013)  
957 investigated the association between delayed mating and fitness, while Pilakouta & Baillet  
958 (2022) assessed whether eagerness to mate is related to temperature.

959

#### 960 (f) Mating success

961 Until now, we have mostly discussed proximate topics that involve individual traits and  
962 decisions, from morphological structures to complex sets of behaviours. Yet, sexual selection  
963 (and evolution of sexual traits) only occurs when intrasexual competition and mate choice  
964 produce variation in individuals' fitness. Darwin (1871) proposed that this occurs when these  
965 mechanisms produce skewed mating success, in which only a portion of the best competitors  
966 (through force or looks) mate and leave descendants (but see section III.5.i). We found a total  
967 of 23 questions focusing on mating success, from 21 meta-analyses (Figure 7). Most of these  
968 questions are related to sexual traits and mechanisms of sexual selection, which have already

969 been discussed in previous topics (see above). Other questions in this category explore  
970 whether mating success is linked to body size (e.g. Sokolovska, Rowe & Johansson, 2000;  
971 Kim *et al.*, 2021) or to specific conditions (e.g. density and sex ratio: Nieberding & Holveck,  
972 2017; lek size: Isvaran & Ponkshe, 2013; parasitism: Hasik & Siepielski, 2022; temperature:  
973 Pilakouta & Baillet, 2022).

974

#### 975 (g) Mating patterns

976 While mating success refers to the number of mates obtained (ignoring these mates' traits),  
977 mating patterns refer to the arrangement of individuals observed mating (or paired) in relation  
978 to their traits. Mating patterns can be influenced by different elements, from mechanisms of  
979 sexual selection (intrasexual competition and mate choice) to temporal or spatial segregation  
980 (Jiang, Bolnick & Kirkpatrick, 2013). This means that studies on mating patterns usually  
981 concentrate on what is observed (often in the field), not necessarily how these patterns  
982 happened. Non-random mating patterns are referred to as assortative or disassortative mating,  
983 in which traits of mating individuals are positively or negatively related, respectively. Thus,  
984 all 14 meta-analytical questions (each from a different study) that fitted this category (Figure  
985 7) explicitly mention assortative or disassortative mating.

986 Many questions from this topic investigated whether non-random mating patterns  
987 occur in respect to a specific trait, such as body size (Arnqvist *et al.*, 1996; Graham *et al.*,  
988 2015; Green, 2019), relatedness (Ihle & Forstmeier, 2013; Pike, Cornwallis & Griffin, 2021),  
989 major histocompatibility complex (Winternitz *et al.*, 2017), or population or species identity  
990 (Randler, 2008; Rometsch *et al.*, 2020; with some specifically testing population isolation on  
991 reproductive isolation: Florin & Ödeen, 2002; Yukilevich, 2012). Conversely, other questions  
992 were unrestricted regarding traits evaluated (e.g. Jiang *et al.*, 2013; Janicke *et al.*, 2019;  
993 Wang *et al.*, 2019; Rios Moura *et al.*, 2021), with some of them assessing whether observer

994 bias (Wang *et al.*, 2019) and sample pooling methods (Rios Moura *et al.*, 2021) were  
995 associated with estimates observed. Lastly, Janicke *et al.* (2019) verified whether assortative  
996 mating is related to species richness.

997

#### 998 (h) Divorce and extra-pair patterns

999 All topics discussed so far are relevant for the entire animal kingdom (although taxa are  
1000 unequally investigated, see section III.2.a). Here, however, we discuss divorce, extra-pair  
1001 copulations (hereby EPCs), and extra-pair paternity (hereby EPP), which pertain to a specific  
1002 niche in the sexual selection literature that applies only to socially monogamous animals  
1003 (forming exclusive social pairs for reproduction). In this context, divorce means re-pairing  
1004 with another individual whilst the previous partner is still alive (Choudhury, 1995), whereas  
1005 EPP refers to fertilizations from EPCs (i.e. copulas outside of the social bond; Griffith,  
1006 Owens & Thuman, 2002). Altogether, this category gathered 16 questions from 16 meta-  
1007 analyses (Figure 7).

1008         Only three meta-analytical questions involved divorce, verifying the association  
1009 between this behaviour with breeding failure before and/or after its occurrence (Dubois &  
1010 Cézilly, 2002; Culina *et al.*, 2015; Culina & Brouwer, 2022). Other questions in this category  
1011 explored the relationship between EPCs or EPP and certain traits, such as age (Cleasby &  
1012 Nakagawa, 2012), ornaments or sexual signals (Table S5), parental care (Arnqvist &  
1013 Kirkpatrick, 2005; Albrecht, Kreisinger & Piálek, 2006), pair relatedness (Arct, Drobnik &  
1014 Cichoń, 2015; Hsu *et al.*, 2015), or a mix of these traits (Møller & Ninni, 1998; Akçay &  
1015 Roughgarden, 2007). In addition, a couple of these studies also tested whether offspring  
1016 fitness is associated with its genetic origin (intra- vs extra-pair; Arnqvist & Kirkpatrick, 2005;  
1017 Akçay & Roughgarden, 2007).

1018

1019 (i) Sexual conflict and estimates of sexual selection

1020 Here, we briefly review the 14 meta-analytical questions (each from a different study) that  
1021 focused on the two remaining topics related to sexual selection: sexual selection estimates  
1022 (see Fitze & le Galliard, 2011; Henshaw, Kahn & Fritzsche, 2016; Anthes *et al.*, 2017) and  
1023 interlocus sexual conflict (Parker, 1979; Chapman *et al.*, 2003) (Figure 7).

1024 Two meta-analytical studies explored sexual selection on traits using standardised  
1025 selection gradients ( $\beta$ : regression between standardised trait values and relative fitness, Lande  
1026 & Arnold, 1983). As a fitness proxy, Hoekstra *et al.* (2001) used mating success, whilst  
1027 Dougherty & Shuker (2016) used both mating and insemination success. Other estimates of  
1028 sexual selection, such as Bateman's gradient ( $\beta_{ss}$ : average reproductive success gains from  
1029 each additional mating; Bateman, 1948) and opportunity of sexual selection ( $I_s$  or  $I_{mates}$ :  
1030 variance in relative mating success; Wade, 1979; Shuster & Wade, 2003), were much more  
1031 common in our dataset (Table S5). Macedo-Rego *et al.* (2020a, 2020b) also used the Jones'  
1032 index ( $s'_{max}$ ; Jones, 2009), albeit Rios Moura & Peixoto (2013) made their own estimate ( $I_{dir}$ :  
1033  $I_s$  if mating were random minus observed  $I_s$ ). Aside from verifying the mean estimates of  
1034 sexual selection found in the literature, several meta-analyses investigated whether these  
1035 estimates were associated with other variables, like availability of reproductive sites (Alissa,  
1036 2018), monopolisation of mates (Macedo-Rego *et al.*, 2020b), operational sex ratio (Rios  
1037 Moura & Peixoto, 2013; Janicke & Morrow, 2018), sexual size dimorphism (Janicke &  
1038 Fromonteil, 2021), and species richness (Janicke *et al.*, 2018). Yet, estimates of sexual  
1039 selection present several constraints regarding how they are computed, which was the main  
1040 subject of some meta-analyses (e.g. how mating success is measured and whether zero  
1041 mating success is included; Anthes *et al.*, 2017; Macedo-Rego *et al.*, 2020a). Note that these  
1042 estimates of sexual selection do not actually take into consideration effects of mate quality  
1043 (see Fitzpatrick, 2015).

1044 At last, we found two meta-analytical studies with unique perspectives in the  
 1045 literature. First, Cally *et al.* (2019) assessed fitness consequences on a population level from  
 1046 experiments that enforced monogamy or manipulated adult sex ratio, essentially modulating  
 1047 sexual selection. Second, Gómez-Llano *et al.* (2023) evaluated the costs imposed by one  
 1048 sex's on the fitness of the other sex through direct (e.g. traumatic insemination) and/or  
 1049 indirect (e.g. harassment) harm, the only study on sexual conflict in our dataset.

1050

1051 *(6) Further challenges and recommendations*

1052 Conducting a meta-analysis on a topic related to sexual selection can be an arduous process.  
 1053 This is because this field presents many conceptual and analytical challenges that are rarely  
 1054 addressed. In this section, we discuss these challenges and provide recommendations for  
 1055 future work in the field of sexual selection, both for empiricists and researchers conducting  
 1056 meta-analyses (summarised in Table 2, see also Nakagawa *et al.*, 2017).

1057

1058 Table 2. Recommendations for meta-analytical research projects on topics related to sexual  
 1059 selection. Some of these recommendations can also be applied on projects with other  
 1060 methodological approaches in this field (in grey). FAIR stands for Findable, Accessible,  
 1061 Interoperable, Reusable (see Wilkinson *et al.*, 2016).

Item	Summarised recommendations	Manuscript section(s)
Research team	<ul style="list-style-type: none"> <li>Form diverse and inclusive research teams (e.g. gender equal)</li> <li>Consider inviting researchers from the Global South for collaborations</li> </ul>	III.6.d
Research question and scope	<ul style="list-style-type: none"> <li>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</li> </ul>	III.2.a, III.2.e, III.5

	<ul style="list-style-type: none"> <li>Exclude humans as a study species if the synthesis also involves other animals</li> </ul>	III.2.b, III.6.a
	<ul style="list-style-type: none"> <li>Avoid limiting (<i>a priori</i>) the study to only males (or only females for mate choice)</li> </ul>	III.2.f
	<ul style="list-style-type: none"> <li>Use the PECOS framework to formalise a research question</li> </ul>	III.6.b
	<ul style="list-style-type: none"> <li>Be aware of the trade-offs from the chosen scope</li> </ul>	
Preregistration or protocol	<ul style="list-style-type: none"> <li>Develop a plan for the study and make it publicly available before conducting it</li> </ul>	III.3.f
	<ul style="list-style-type: none"> <li>Use different search sources (e.g. multiple databases), including grey literature</li> </ul>	
Data search	<ul style="list-style-type: none"> <li>Provide search details, such as the dates on when it was conducted and the exact queries with Boolean operators used</li> </ul>	III.3.a
	<ul style="list-style-type: none"> <li>Provide the number of retrieved, included, and excluded studies at every step of the screening process</li> </ul>	
Screening process	<ul style="list-style-type: none"> <li>Provide individual justification for study exclusions at the full-text screening stage</li> <li>Make a PRISMA-like figure to summarise the screening process</li> </ul>	III.3.b
	<ul style="list-style-type: none"> <li>Use appropriate software (e.g. R packages <i>metafor</i> or <i>MCMCglmm</i>)</li> </ul>	III.3.c
	<ul style="list-style-type: none"> <li>Deal with statistical non-independence (e.g. from phylogeny and shared studies)</li> </ul>	
	<ul style="list-style-type: none"> <li>Quantify heterogeneity</li> </ul>	III.3.e
Analysis	<ul style="list-style-type: none"> <li>Test for publication bias</li> </ul>	
	<ul style="list-style-type: none"> <li>Ensure that the meta-analytical model reflects the main question</li> </ul>	III.6.c
	<ul style="list-style-type: none"> <li>Use moderators to explore sources of heterogeneity and to answer smaller questions</li> </ul>	
Code and data sharing	<ul style="list-style-type: none"> <li>Provide all data used in the study (preferentially in a separate FAIR file rather than in a table in the study)</li> </ul>	III.3.d



- Provide metadata for all data shared (in a separate file)
- Provide analysis scripts

1062

1063 (a) Inclusion of humans

1064 Darwin's (1871) book "The descent of man, and selection in relation to sex" addresses  
1065 human evolution and sexual selection (Ruse, 2015). At times, Darwin (1871) explicitly mixed  
1066 these topics, using several examples from human society to support his arguments related to  
1067 sexual selection. Using our own experiences to understand nature is intuitive (Kokko, 2017),  
1068 and perhaps many scientists believe that studying other animals' reproductive behaviours can  
1069 help us to comprehend ourselves. However, we show a distinct aspect from other animals: an  
1070 extremely complex culture that has a strong effect on our behaviours, including the ones  
1071 related to reproduction (Eagly & Wood, 1999). For instance, culture influences which  
1072 phenotypes are deemed attractive (Silverstein *et al.*, 1986) and pair formation can be  
1073 subjected to the decision of others (e.g. parents' influence; Buunk, Pollet & Dubbs, 2012).  
1074 Additionally, people may choose to have few or no children through celibacy, contraception  
1075 methods, or abortion, meaning that reproductive success plainly loses its utility in sexual  
1076 selection studies when compared with other organisms.

1077       Issues from including humans in meta-analyses of sexual selection are not only  
1078 problematic for behavioural traits: selection on humans has been modified or even nullified  
1079 as we increasingly control our environment. For instance, crooked teeth in humans became  
1080 common only recently, after we started eating processed (soft) foods that relaxed selection for  
1081 large jaws that could accommodate all of our teeth (Corruccini, 1984; Lieberman *et al.*,  
1082 2004). Thus, even for traits that are not under direct influence of culture (e.g. sperm traits),  
1083 the distinct evolutionary pressures on modern humans might mislead comparisons with other

1084 organisms. This argument also applies for domesticated animals, as the process of artificial  
1085 selection applied on them can modify their traits, as noted by Mautz *et al.* (2013).

1086 We ultimately recommend to evolutionary biologists to exclude humans from meta-  
1087 analyses on topics related to sexual selection with other animals for the reasons above.  
1088 Furthermore, the thought of humans as “just another species” is humble, but can also lead to  
1089 anthropomorphisation of other organisms. This might be especially relevant for how we think  
1090 of males and females (and their reproductive patterns; see section III.2.f), as our gender  
1091 notions may affect our perceptions of them (Ahnesjö *et al.*, 2020; Pollo & Kasumovic, 2022).  
1092 For example, Darwin (1871) argued that women are inferior to men, among other conclusions  
1093 based on his observations from the Victorian society he lived in, which were described as  
1094 processes emerging from our biology. A potential consequence of this type of rationale is  
1095 falling into a vortex of self-affirmation, in which our societal views influence our notion of  
1096 sex differences in nature and *vice versa*. In fact, part of the field of evolutionary psychology,  
1097 a field born out of evolutionary biology from the 1970s (strongly based on Trivers, 1972; see  
1098 also Fausto-Sterling *et al.*, 1997), seems to have succumbed to this pattern as they recurrently  
1099 overemphasise gender differences (Eagly & Wood, 1999; Stewart-Williams & Thomas,  
1100 2013). Studies from evolutionary psychologists commonly rely on assumptions related to  
1101 other animals and ancestral human societies (for which information is scarce) to make  
1102 hypotheses on current human behaviours (e.g. Geary, 2021). For instance, Lewis *et al.* (2017)  
1103 claimed that high-heels make women more attractive because they can increase women’s  
1104 lumbar curvature, representing a morphological adaptation for child bearing that would  
1105 ultimately signal their high-quality to men. Lewis *et al.* (2017), however, barely mentioned  
1106 alternative non-biological explanations to why women are deemed more attractive in high  
1107 heels (e.g. influence of media). In addition, the authors completely ignored any historical  
1108 relevant facts about high-heels, including that they were also used by men and were a symbol

1109 of masculinity for seven centuries before being associated with femininity in the 18th century  
1110 (Semmelhack, 2020). This shows that reducing human behaviours to a simple biological  
1111 product, which is an assumption implicitly made by meta-analyses related to sexual selection  
1112 that include them with other species, can have profound consequences. If researchers strongly  
1113 disagree with our stance of excluding humans from meta-analyses with other animals, we  
1114 suggest that they at least include additional analyses, in which effect sizes obtained from  
1115 humans are subsetting to assess their role in the study's conclusions (as in Fromonteil *et al.*,  
1116 2023).

1117

#### 1118 (b) Conceptual challenges and recommendations

1119 Darwin (1859, 1871) founded the field of sexual selection using jargon: he extensively used  
1120 the terms “primary sexual characters” and “secondary sexual characters” in his work  
1121 (attributing their creation to the surgeon and anatomist John Hunter). These terms, mainly  
1122 secondary sexual characters, served as the backbone for Darwin's arguments on the existence  
1123 of sexual selection. Whilst primary sexual characters refer to traits necessary for reproduction  
1124 (e.g. gonads and genitalia), secondary sexual characters were used by Darwin to refer to traits  
1125 that would supposedly be linked to mate acquisition but not reproduction itself. Secondary  
1126 sexual characters are usually classified as ornaments (mate attraction) or weapons  
1127 (intrasexual combat), which also became ubiquitous terms in the literature related to sexual  
1128 selection (e.g. Andersson, 1994; Andersson & Iwasa, 1996; Andersson & Simmons, 2006;  
1129 Shuker, 2010; Hosken & House, 2011; Simmons, Lüpold & Fitzpatrick, 2017; Lindsay *et al.*,  
1130 2019). Such popularity can also be seen for the term “sexual signal” (whose exact origin is  
1131 unknown to us, but probably from the 1980s; e.g. Endler & McLellan, 1988; Endler, 1992),  
1132 which highlights the communicative function (i.e. role in inter-individual interactions) of  
1133 secondary sexual traits.

1134           Researchers interested in related topics to sexual selection commonly employ this  
1135 jargon when describing their question and selection criteria in meta-analyses. However, the  
1136 expressions mentioned above are vague and loosely used, potentially causing transparency  
1137 issues. For instance, numerous traits are frequently classified as secondary sexual  
1138 characteristics simply based on sexual dimorphism, without a proper examination of its role  
1139 on mate acquisition or reproductive success. This practice creates problematic cases, such as  
1140 body size, which is explicitly mentioned as a secondary sexual trait by some (e.g. Simmons *et*  
1141 *al.*, 2017). Although indeed there is evidence that males in many species benefit from larger  
1142 bodies in male-male contests, leading to sexual selection on this trait and sometimes male-  
1143 biased size dimorphism (Andersson, 1994), this pattern is simply assumed at times. An  
1144 example can be seen in Moore & Wilson (2002), who relied exclusively on sexual size  
1145 dimorphism as a proxy for sexual selection without evidence that body size was truly relevant  
1146 to reproduction in all species investigated. The precarity of this assumption becomes evident  
1147 when several cases of sexual size dimorphism occur due to other types of selection on body  
1148 size, such as fecundity selection resulting in females larger than males in many invertebrates  
1149 (but see Pincheira-Donoso & Hunt, 2017). Furthermore, if secondary sexual characteristics  
1150 are synonymous with sexually selected traits (see Wiens & Tuschhoff, 2020), then this term  
1151 could also encompass primary sexual traits, which are often under sexual selection (e.g.  
1152 genitalia can play a role in post-copulatory competition; Andersson & Simmons, 2006).  
1153 Similarly, traits related to gametes (e.g. sperm velocity) appear to be in a conceptual limbo,  
1154 as they are rarely associated with this lingo despite also being determinant for post-  
1155 copulatory processes (but see Rico-Guevara & Hurme, 2019).

1156           Mentioning sexual ornaments also requires clarification, as this expression simply  
1157 alludes to shiny, elaborate, or extravagant traits used to attract mates. The fact that the word  
1158 ornament has a colloquial meaning that predates its scientific (sexual) meaning is not a

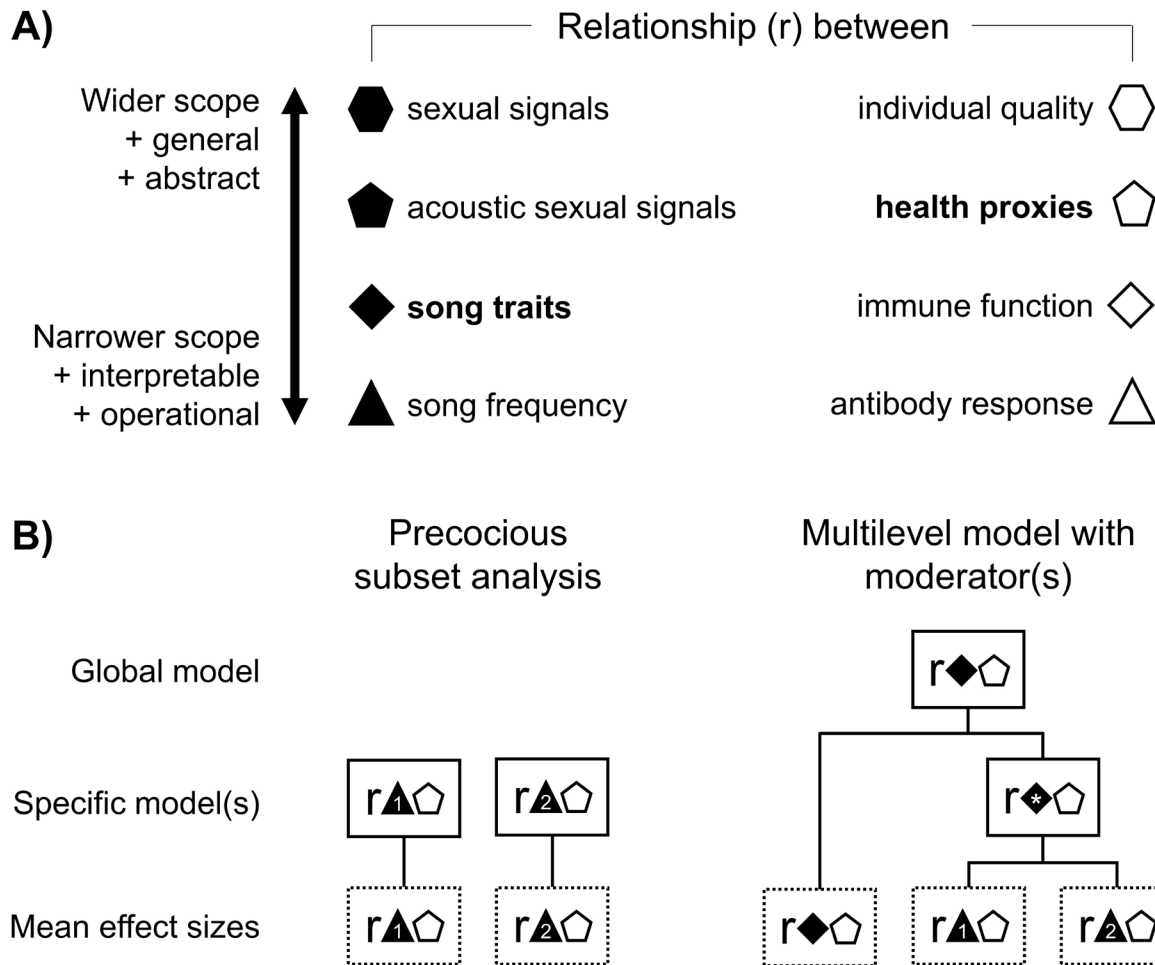
1159 coincidence: we tend to be fascinated by what catches our eyes or ears, revealing that our  
1160 own sensory bias might not be reliable to describe all traits and patterns existing in nature.  
1161 Thus, at least theoretically, other kinds of traits (e.g. chemical, tactile, electric; Kramer, 1990;  
1162 Johansson & Jones, 2007) can also be classified as ornaments despite being inconspicuous to  
1163 us. Although we cannot escape our human condition when observing nature (see Kokko,  
1164 2017), it is crucial to acknowledge our biases, especially in meta-analyses that claim to  
1165 explore general patterns related to sexual ornaments (section III.5.a). This also applies for  
1166 other terms, such as weapons and sexual signalling, which tend to be used for morphological  
1167 structures and acoustic displays, respectively. Moreover, sexual ornaments and sexual signals  
1168 seem to be overlapping concepts, although the latter might also encompass signals used  
1169 during agonistic encounters (e.g. threat signals). Overall, the many inconsistencies in the use  
1170 of these expressions reveal that their careless application can be dangerous and misleading.

1171         Ultimately, the words researchers choose to describe their questions are pivotal  
1172 because they define its scope and the required degree of detailing what exactly is being  
1173 studied. The specific expressions linked to sexual selection we mentioned in this section tend  
1174 to be quite abstract and thus represent a wider scope than specific terms that depict direct  
1175 measurements (e.g. sexual signal vs. song frequency, respectively; Figure 16). The larger the  
1176 scope of a question, the more likely the diversity of measurements included in a meta-  
1177 analytical study will be (e.g. more distinct traits, methods, taxa), increasing the apparent  
1178 generality of the results at the cost of its interpretability (Figure 16; Spake *et al.*, 2022). The  
1179 fact that many meta-analyses have a wide scope possibly explains the common pattern of  
1180 high heterogeneity found in meta-analytical studies in ecology and evolution (Senior *et al.*,  
1181 2016a). Greater heterogeneity means that a global effect size has less reliability and that  
1182 moderators are decisive in understanding patterns (Spake *et al.*, 2022). In other words, the  
1183 motto invoked by biologists “it depends” intensifies with heterogeneity. However, studies

1184 with wide scope questions receive more attention and usually get published in prestigious  
1185 journals precisely because they claim to settle theoretical conundrums with a single, concise  
1186 estimate. Such a practice means that the studies that carry the most responsibility to untangle  
1187 complex patterns are commonly the ones that highlight superficial results while downplaying  
1188 their limitations. For instance, García-Roa *et al.* (2020) claimed to examine the effect of  
1189 temperature on sexual selection, but details of their dataset could only be found in their  
1190 supplementary material (very little information in-text). A closer inspection on their data  
1191 reveals that most effect sizes for females were based on fecundity, which is far from being  
1192 strictly related to sexual selection, casting doubt on the general validity of García-Roa *et al.*  
1193 (2020)'s claims. Many other meta-analysis in our systematic map show a similar problem,  
1194 asking wide scope questions with unclear sexual traits or sexual selection proxies (e.g. Møller  
1195 & Alatalo, 1999; Møller, Christe & Lux, 1999; Weir *et al.*, 2011; Cally *et al.*, 2019; Hasik &  
1196 Siepielski, 2022).

1197         As we showed, the specific expressions linked to sexual selection refer to diverse  
1198 traits and patterns found in nature, being inherently loosely defined. Researchers thus need to  
1199 be careful when using these terms in meta-analyses, clarifying what they truly encompass so  
1200 readers can understand their study's focus and limitations. Clarification can be done by  
1201 choosing the appropriate words that describe their research questions and goals (Figure 16) as  
1202 well as by showing detailed information on the data searched and utilised in the manuscript  
1203 (not just in the supplementary material). Finally, we emphasise that, as the scope of a  
1204 question (and consequently of the study) gets wider, moderators and meta-regressions  
1205 become increasingly necessary to avoid false generalisations (Nakagawa *et al.*, 2017; Spake  
1206 *et al.*, 2022; see section III.6.c).

1207



1208

1209 Figure 16. Meta-analytical challenges in sexual selection using (Garamszegi, 2005) as an  
 1210 example. Panel A shows how the scope of a question (e.g. whether two variables are related,  
 1211 denoted as “r”) is associated with the exact words used to describe it, in which shapes with  
 1212 more vertices represent wider scope. Terms in bold highlight our suggestion for a general  
 1213 question in (Garamszegi, 2005) (see text). Panel B illustrates possible analytical  
 1214 implementations, with different options of meta-analytical models (solid line boxes) and their  
 1215 respective estimated mean effect sizes (dotted line boxes). A multilevel model with  
 1216 moderator(s) is recommended to estimate a global mean effect size that matches a general  
 1217 question (see text). Numbers inside shapes represent different subgroups (e.g. 1 = song  
 1218 frequency, 2 = song complexity), while a star (\*) inside a shape represents the use of a  
 1219 moderator within a meta-analytical model.

1220

1221 (c) Analytical challenges and recommendations

1222 Several papers and books specifically targeted at ecology and evolutionary biologists provide  
1223 helpful recommendations on how to conduct meta-analyses. Their focus ranges from initial  
1224 procedures that are also part of systematic reviews (e.g. search and screening) to specific  
1225 statistical methods (e.g. Nakagawa & Cuthill, 2007; Nakagawa & Santos, 2012; Koricheva *et*  
1226 *al.*, 2013; Noble *et al.*, 2017; Foo *et al.*, 2021; O’Dea *et al.*, 2021; Nakagawa *et al.*, 2021;  
1227 Spake *et al.*, 2022; Yang *et al.*, 2023b). Nonetheless, we noticed that many meta-analyses  
1228 included in our systematic map conduct precocious subset analyses (i.e. practice of  
1229 partitioning the extracted data and then fitting a separate meta-analytical model on each  
1230 subset without a global model; Figure 16). This procedure often leads to a mismatch between  
1231 the general question asked in the study and its respective statistical analysis. In this section,  
1232 we use a fairly simple meta-analysis (Garamszegi, 2005) to illustrate our argument.

1233 Garamszegi (2005) examined the relationship between distinct bird song traits and  
1234 health proxies (e.g. parasite prevalence or immune function). Intuitively, one can assume that  
1235 this study asks “is song expression associated with health proxies?”. Yet, Garamszegi (2005)  
1236 shattered the expectation of a single answer (e.g. through a global mean effect size) by  
1237 presenting four separate mean effect sizes, each related to a different song trait (performance,  
1238 complexity, duration, and frequency). This exemplifies precocious subset analysis, and we  
1239 argue that this approach generates two issues.

1240 First, the reader is left without an answer to a general question (even if it is a vague  
1241 one). Garamszegi (2005) only provides answers to separate, specific questions (e.g. does song  
1242 frequency reflect health?; does song complexity reflect health?; etc). Second, subset analysis  
1243 could increase error type I (i.e. rejecting a null hypothesis that is actually true) when  
1244 compared with a unified, random-effects (multilevel) model (cf. Nakagawa & Santos, 2012;



1245 Nakagawa *et al.*, 2022). Third, effect sizes from groups analysed with different models  
1246 cannot be statistically compared. Fourth, it limits the test of other moderators and their  
1247 interactions. For example, Crean & Senior (2019) verified the effect of high-fat diets on  
1248 model mammals regarding different sperm traits and several measurements of reproductive  
1249 success, but each of these traits and measurements (17 in total) was analysed separately,  
1250 meaning that the role of moderators (diet duration, specimen age, etc) could not be assessed  
1251 across all effect sizes (only within each subset). Why analytical fragmentation has been  
1252 employed so often is unclear, but we suspect that researchers' concern of being accused of  
1253 making unfair comparisons through wider-scope models has increased the use of this  
1254 approach. Alternatively, researchers may simply believe that each sub-question requires a  
1255 separate meta-analytical model. Regardless of the reason, we believe it is crucial to discuss  
1256 the benefits and disadvantages of each approach.

1257         Analysing data separately may seem fair at first glance: meta-analyses are often  
1258 criticised for clumping conceptually distinct data to make inferences (i.e. "mixing apples and  
1259 oranges"; Arnqvist & Wooster, 1995; Noble *et al.*, 2022). Although meta-analyses in other  
1260 fields are not exempt from this complaint, the diversity of methodologies, biological traits,  
1261 mechanisms, and patterns across species and empirical studies makes meta-analyses in the  
1262 field of ecology and evolution particularly prone to this criticism. However, researchers have  
1263 little option other than categorising measurements to make comparisons. For example,  
1264 although Garamszegi (2005) analysed song traits separately, each one of them still included  
1265 different measurements (e.g. song frequency involved both lowest and highest frequency, as  
1266 well as frequency range). Moreover, parasite prevalence and immune function were analysed  
1267 together, revealing that this author deemed them analogous measurements. Therefore,  
1268 subsetting the analysis did not avail Garamszegi (2005) to entirely escape from mixing apples  
1269 and oranges, essentially because it is inevitable to do so to a certain extent (Rosenthal, 1991).

1270 We suggest to researchers to, foremost, carefully define a question using the  
1271 PECO/PICO framework (Richardson *et al.*, 1995; Foo *et al.*, 2021) that encapsulates all  
1272 subquestions (if possible). Although multiple specific questions can be asked in a single  
1273 meta-analytical study, they often can be summarised into a more general one, as we have  
1274 shown for Garamszegi (2005) (Figure 16). This allows researchers to conduct one or few  
1275 models with predictors (i.e. moderators) that can potentially explain the variation found,  
1276 emphasising their effectiveness or lack thereof in doing so (Spake *et al.*, 2022), instead of  
1277 fragmenting the data and analysis into multiple subsets from the start (Figure 16). These  
1278 moderators fundamentally work as the specific questions that many authors ask when using  
1279 subset analyses. A global model, however, becomes inadvisable when sub-questions are  
1280 completely unrelated to one another so a more general question becomes infeasible (although  
1281 this might be subjective) or when effect sizes calculated are distinct in nature (based on  
1282 means vs. based on variances). This approach makes it even more critical that authors specify  
1283 the direction of calculated effect sizes for each measurement before analysis, preferably  
1284 based on grounded hypotheses (e.g. Dougherty, 2021a). Nonetheless, the direction of effect  
1285 sizes can be modified ad-hoc if one of the subsets presents an opposite pattern, so that the  
1286 global mean effect size can focus on magnitude rather than direction.

1287 Researchers might still harbour suspicion over a global model approach in complex  
1288 cases as, until now, we have only used a meta-analysis with relatively specific questions as an  
1289 example (Garamszegi, 2005). Thus, consider Alissa (2018), who asked whether limitation in  
1290 reproductive sites is associated with several measurements related to sexual selection (e.g.  
1291 pre-copulatory intrasexual competition, sperm competition, selection on male traits, and  
1292 opportunity for sexual selection). In this study, the author conducted several meta-analyses  
1293 (i.e. subsets were independently analysed), probably because of wildly distinct measurements  
1294 included in it. Although it would not be possible to combine opportunity for sexual selection

1295 with the other measurements because they are represented by distinct types of effect sizes in  
1296 the study (lnCVR and Zr, respectively), all else could be grouped together. Grouping the  
1297 effect sizes to estimate a single mean effect size would allow the author to compare the effect  
1298 sizes for each measurement related to sexual selection. In truth, this global effect size would  
1299 represent a more abstract and less interpretable estimate: whether reproductive site limitation  
1300 is associated with various measurements related to sexual selection (see section III.6.b).  
1301 However, the existence of a global mean effect size does not preclude researchers to focus on  
1302 specific, narrow questions, which can be done with moderators and meta-regressions. Doing  
1303 so would maintain the original conceptual structure in Alissa's (2018) manuscript while  
1304 correcting its analysis.

1305         Our recommendation to unify multiple, usually related questions to fit a single (or as  
1306 few as possible) meta-analytical model does not mean to incentivize wider questions, but  
1307 rather attempts to streamline analyses. In fact, focused meta-analyses (i.e. with narrow  
1308 questions) can be more reliable because they are easy to interpret (Figure 16). Conversely, as  
1309 previously mentioned (see section III.6.b), studies with wide questions that employ few or no  
1310 meta-regressions might be of little use if they show highly heterogeneous estimates. Although  
1311 the use of moderators might be constrained (e.g. due to too few data points), authors should at  
1312 least justify these limitations and consider them to avoid misleading conclusions.

1313

#### 1314 (d) Authorship diversity

1315 Our bibliometric analysis suggests that authors conducting meta-analyses on topics associated  
1316 with sexual selection are often men based in developed countries (see section III.4), which is  
1317 a pattern often found in academia (Astegiano, Sebastián-González & Castanho, 2019; Huang  
1318 *et al.*, 2020). We note, however, that our analysis regarding countries is purely based on  
1319 affiliations listed, meaning that authors could be of a different nationality (i.e. immigrants).

1320 For instance, although four of the authors of the present study are affiliated to the same  
1321 Australian university, none was born in Australia. Still, the existence of international and  
1322 intercontinental collaborations we found reiterate the globalisation of science (Gui, Liu & Du,  
1323 2019), although concentrated in the Global North (i.e. developed countries).

1324         While patterns of research production for countries may follow economic trends (e.g.  
1325 amount of public funding to research in each country; Gush *et al.*, 2018), gender inequity in  
1326 research production has multiple explanations. First, it might be a consequence of a “leaky  
1327 pipeline” that precludes women from filling higher academic positions as often as men (Shaw  
1328 & Stanton, 2012; McDermott *et al.*, 2018). This is also seen in boards of scientific societies,  
1329 in which women are outnumbered by men (Potvin *et al.*, 2018). Intuitively, this entails fewer  
1330 opportunities for women to conduct research. In addition, there is a gender gap in  
1331 productivity in which women are outperformed by men, even in gender equal academic  
1332 faculties (Astegiano *et al.*, 2019). This can be a consequence of differential pressures on  
1333 women, compared with men, from inside (e.g. lower salary and more time spent in  
1334 administrative tasks; DesRoches *et al.*, 2010) and outside (e.g. family caring; Fox, Fonseca &  
1335 Bao, 2011) of academia.

1336         The patterns we found regarding countries and gender are not limited to this specific  
1337 literature, but simply another example of a more generalised problem in academia and  
1338 research production overall. Yet, this does not mean we should accept this pattern idly.  
1339 Rather, it emphasises that actions are needed to change this precarious situation as diversity  
1340 can promote creativity (McLeod, Lobel & Cox, 1996) and innovation (Nieto & Santamaría,  
1341 2007), ultimately being beneficial to science (Intemann, 2009; Cheruvilil *et al.*, 2014). The  
1342 most obvious example of benefits brought by diversity in the context of meta-analyses comes  
1343 from the inclusion of people with distinct language skills (e.g. from different countries) that  
1344 can increase the coverage of the literature retrieved beyond just papers in English (Amano *et*

1345 *al.*, 2023). Furthermore, people of distinct nationalities can also vary in how they perceive  
1346 stereotypes related to sexual behaviours in nature, making diverse teams more open to  
1347 various perspectives (Pollo & Kasumovic, 2022).

1348 Several solutions have been proposed to ameliorate these diversity issues. For  
1349 instance, researchers from the Global North should actively and fairly collaborate with  
1350 researchers from the Global South (see more suggestions in Haelewaters, Hofmann &  
1351 Romero-Olivares, 2021 and in Nakamura *et al.*, 2023). Furthermore, many actions are being  
1352 employed by different institutions to address gender disparity observed in academia, but they  
1353 are rarely applied on a large scale or are ineffective (see Casad *et al.*, 2021) and references  
1354 within). Yet, gender and country of affiliation or origin are just a few of several aspects that  
1355 matter to diversity. For instance, people of colour (Evangelista *et al.*, 2020) and from lower  
1356 economic backgrounds (Lee, 2016) are commonly excluded from academia, revealing a need  
1357 to develop ways to include these marginalised groups as well.

1358

#### 1359 (e) Beyond meta-analyses

1360 Throughout our manuscript, we identified several biases related to the content of meta-  
1361 analyses on topics related to sexual selection (e.g. on specific questions, taxonomic groups,  
1362 focal sex, etc). However, this might simply be a reflection of biases that already occur in the  
1363 primary literature on sexual selection. For instance, although researchers might be interested  
1364 in meta-analytical questions that can encompass all animals, data available are highly  
1365 concentrated in certain animal groups (e.g. birds; see section III.2.a). Thus, it might be  
1366 fruitless to expect that researchers interested in meta-analyses can solve these biases alone if  
1367 the raw material (primary evidence) remains unchanged. In fact, proper meta-analyses are  
1368 also systematic reviews, highlighting gaps in the primary literature and therefore serving as  
1369 indicators of the extent of our empirical knowledge.

1370           One source of generalised biases in the literature may lie in the current publishing  
1371 system, which shows an obsession with “novelty” (Cohen, 2017; Brembs, 2019; Ottaviani *et*  
1372 *al.*, 2023). Paradoxically, novelty is rarely defined by journals that request it, but possibly  
1373 refers to new and impactful discoveries, albeit this is highly subjective (Brembs, 2019). On  
1374 one hand, this can encourage the production of meta-analyses because of their great power to  
1375 test hypotheses (but see section III.6.c). Indeed, meta-analytical studies are often published in  
1376 prestigious journals (e.g. Weaver *et al.*, 2018; Nolzco *et al.*, 2022). However, as previously  
1377 mentioned, meta-analyses in ecology and evolution commonly detect high heterogeneity  
1378 among effect sizes and often fail to find factors that can explain it, mainly because data are  
1379 scarce. This means that continuing to generate empirical data is almost always necessary,  
1380 regardless of the subject. Yet, the pursuit of novelty only reduces the reward of further  
1381 empirical research on a topic, especially with methods, organisms (even if not the same  
1382 species or even genus), or results that resemble already published papers. For example, a  
1383 study on mate choice with a spider species becomes less valuable to the publishing system  
1384 the more studies on mate choice there are with other spiders (even though there are more than  
1385 50,000 species of spiders). This perspective makes empirical research harder to publish in  
1386 top-tier journals, ultimately discouraging scientists from producing empirical data that would  
1387 be extremely valuable to build a solid foundation of the theory. In a system that hampers  
1388 research endeavours because of some similarity with previous work, replication becomes  
1389 almost impossible despite being pivotal to science (Kelly, 2006; Nakagawa & Parker, 2015;  
1390 Fraser *et al.*, 2020).

1391           Limited research replication has many negative impacts on meta-analyses. Not only  
1392 does it reduce the amount and robustness of empirical data available, but also precludes  
1393 updates of meta-analyses as this can be seen as “not novel”. Our study actually shows that  
1394 many meta-analyses on topics related to sexual selection should be redone, both because new

1395 data has accumulated since they were published and because of their substandard methods  
1396 and reporting (see section III.3). Moreover, the fact that numerous decisions in a research  
1397 project can generate different outputs (Gelman & Loken, 2013) also applies to meta-analyses.  
1398 For instance, some meta-analytical studies addressed almost identical questions but had their  
1399 own particularities and sometimes reached distinct conclusions (e.g. Pollo *et al.*, 2022;  
1400 Dougherty, 2023). This only emphasises that how research is conducted is as important, if not  
1401 more, than how novel the question or methods are. Therefore, we deem innovation as pivotal  
1402 to advancements in the field of sexual selection as long as it does not sacrifice further  
1403 research of superficially explored topics.

1404

#### 1405 **IV. CONCLUSIONS**

1406 (1) The vastness of the field of sexual selection can be seen in more than 150 meta-analyses  
1407 on topics associated with it. Although the first of these studies was published more than 25  
1408 years ago, most of them were conducted in the last decade.

1409 (2) We found numerous biases in these meta-analytical studies. Most of them concentrated on  
1410 birds or insects (taxonomic bias) and on male traits or patterns (conforming sex bias).  
1411 Furthermore, although the questions asked in these studies were diverse, many concentrated  
1412 on pre-copulatory sexual traits, such as weapons and ornaments. Thus, we call for greater  
1413 research attention to females, underexplored animals, and neglected topics such as post-  
1414 copulatory processes.

1415 (3) The reporting quality of meta-analyses in the field of sexual selection is often poor,  
1416 indicating that many might be unreliable. This problem is particularly strong for sharing of  
1417 raw data and analysis scripts, revealing a dire need to improve these issues in future meta-  
1418 analyses.

1419 (4) We observed both geographical and gender bias in respect to researchers that conducted  
1420 meta-analyses on topics related to sexual selection. Specifically, most of these papers were  
1421 authored by men based in developed countries, signalling that gender and socio-cultural  
1422 diversity might be lacking in the field of sexual selection. This reiterates the need for  
1423 including minority groups in academia.

1424 (5) We noticed that meta-analyses on topics related to sexual selection commonly employ  
1425 detrimental conceptual and methodological approaches. We therefore recommend to authors  
1426 to avoid including humans with other species in meta-analytical studies in this field, to be  
1427 careful with loose terms that are part of the sexual selection jargon, and to use global meta-  
1428 analytical models with moderators to make inferences. This, however, should be a  
1429 consequence of a well thought plan that starts at the inception of the study, with a well  
1430 formulated question and specific hypothesis.

1431 (6) Despite our focus on meta-analyses, many of the issues pointed out here can be an  
1432 extension of problems occurring in the primary literature (content) and in academia (authors).  
1433 Thus, our manuscript possibly serves as a status report for the whole field of sexual selection.

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## 1440 **VI. AUTHOR CONTRIBUTIONS**

1441 Conceptualisation: P.P., M.L., S.N.; data curation: P.P.; formal analysis: P.P.; funding  
1442 acquisition: S.N.; investigation: P.P., M.L., Y.Y., A.C., S.N.; methodology: P.P., M.L., S.N.;



1443 project administration: P.P., S.N.; software: P.P.; supervision: S.N.; visualisation: P.P.;  
1444 writing - original draft: P.P., S.N.; writing - review & editing: P.P., M.L., Y.Y., A.C., S.N.

1445

## 1446 **VII. DATA AVAILABILITY**

1447 The supplementary material is available at [https://pietropollo.github.io/map\\_sexual\\_selection](https://pietropollo.github.io/map_sexual_selection).

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