

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 conducted 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. Moreover, the topics in these studies
23 varied immensely, from proximate (e.g. relationship of ornaments with other traits) to
24 ultimate questions (e.g. formal estimates of sexual selection strength), albeit the former were
25 more common. We also observed several common issues in these studies, such as lack of

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

41

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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. Our
155 study 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 where are researchers that conducted existing meta-analyses? See section
167 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*

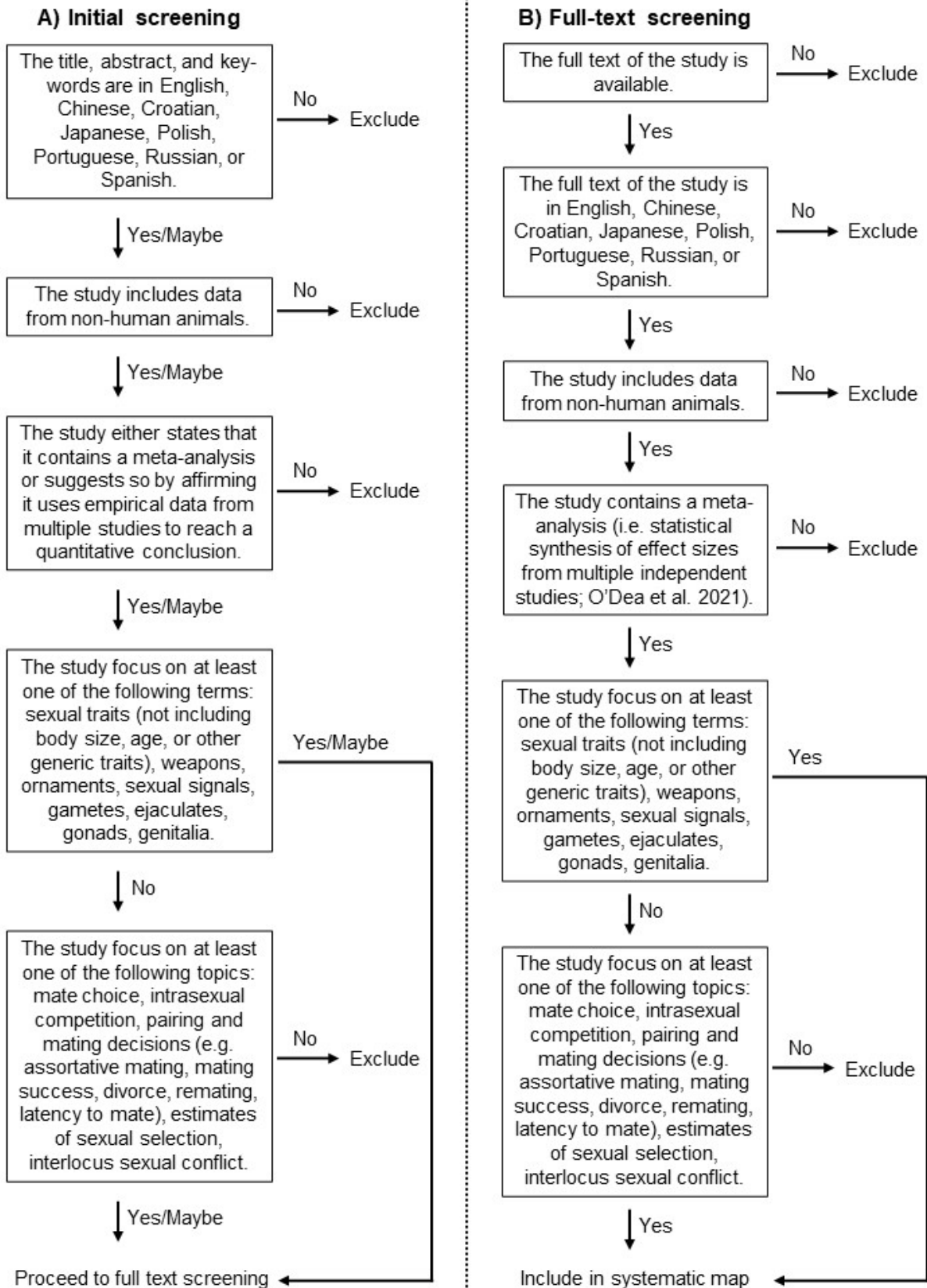
198 Our screening criteria were summarised in Table 1 (but see details in the Supplementary
199 material), while our screening process is shown in Figure 1 (slightly different from the one in
200 our pre-registration but conceptually identical; see Pollo *et al.* 2023). We used Rayyan QCRI
201 (Ouzzani *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.

207

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

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

210



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 in fact relevant to our systematic map (e.g. Goldberg *et*
230 *al.*, 2020) contained questions related to paternal care). Similarly, not all variables used
231 within certain questions were relevant (e.g. Leung & Forbes, 1996) mixed mating success
232 with other fitness measures). Therefore, we took the liberty to select and describe the studies'
233 questions relevant to our systematic map without necessarily relying on the exact words used
234 by their original authors (see further details in Supplementary material). We aimed to extract
235 only questions that we considered central to each meta-analytical study. Because of this, we
236 modified or excluded some variables initially extracted (e.g. how main questions were

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

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

259

260 (b) Reporting appraisal

261 We used PRISMA-EcoEvo (O’Dea *et al.*, 2021) to evaluate reporting and methodological
262 aspects of meta-analyses included in our systematic map. Although PRISMA-EcoEvo only
263 provides guidelines and is not an appraisal tool, other appraisal tools (e.g. Woodcock, Pullin
264 & Kaiser, 2014: CEESAT; Shea *et al.*, 2017: AMSTAR 2) do not include items we aimed to
265 quantify. Therefore, we used the PRISMA-EcoEvo checklist to conduct our reporting
266 appraisal, choosing a subset of the items that are often deemed key aspects for transparency
267 and robustness of meta-analyses, such as registering planned research (Allen & Mehler,
268 2019), detailing the search and screening of studies (McGowan *et al.*, 2016; Palpacuer *et al.*,
269 2019), handling statistical non-independence (Noble *et al.*, 2017), and sharing data (Piccolo
270 & Frampton, 2016), among others (see section III.3). We mainly surveyed whether these
271 elements were described and/or provided, but for specific aspects we also collected detailed
272 information if possible (e.g. which software was used for statistical inferences). Moreover,
273 although our systematic map included meta-analyses in a broad sense (see section II.2), some
274 may be more restrictive on meta-analyses’ definition (Nakagawa *et al.*, 2023a). Thus, we also
275 verified whether studies included in our systematic map were traditional meta-analyses, i.e.
276 used traditional effect sizes and properly modelled heterogeneity using additive weighting
277 (Nakagawa *et al.*, 2023a). We primarily assessed this information based on statistical
278 methods described in studies, including model equations and software used.

279

280 (c) Bibliometrics

281 We extracted author affiliations and names from meta-analyses on topics associated with
282 sexual selection. We retrieved this information from Scopus using the packages *bibliometrix*
283 (Aria & Cuccurullo, 2017) and *rscopus* (Muschelli, 2019) in R (R Core Team, 2022), on
284 August 7th and 14th 2023, respectively. We manually extracted this information for studies
285 that were not yet indexed in Scopus (e.g. theses and recent papers, n = 9). We then

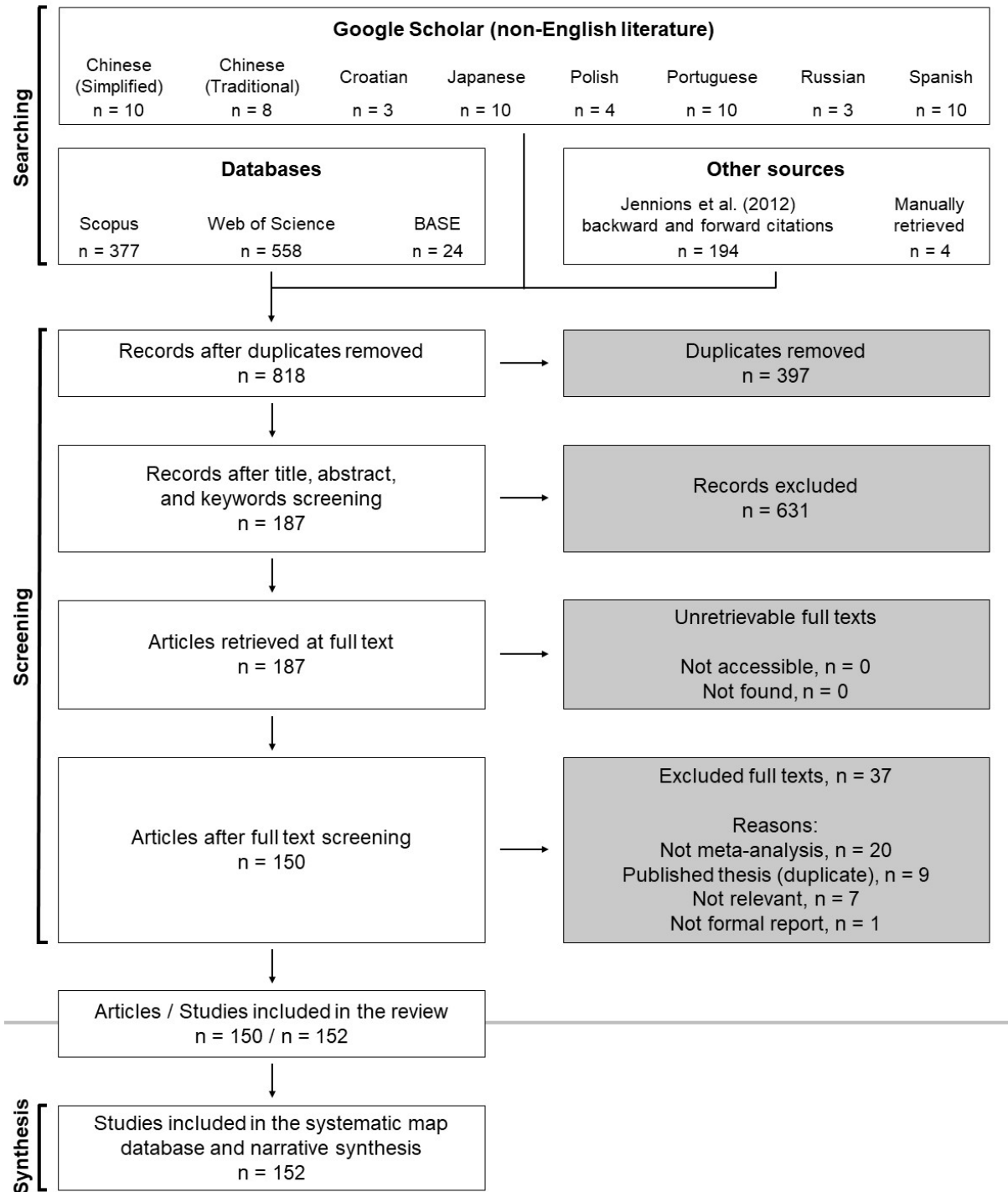
286 determined authors' gender from their first name using the package *genderizeR* (Wais, 2016).
287 Although this approach has its faults (e.g. erroneous label assignment, especially for people
288 that do not identify with binary genders), it includes an estimation of the certainty that a name
289 is associated with a given gender based on real data. Thus, to minimise errors, we only used
290 this automatic labelling when the gender assignment certainty was higher than 95%. For
291 names with ambiguous gender association (i.e. lower certainty), we manually searched the
292 authors' name online to assign gender based on information we could find (e.g. profiles on
293 universities' websites).

294

295 **III. Results and discussion**

296 *(1) Number of eligible meta-analytic studies*

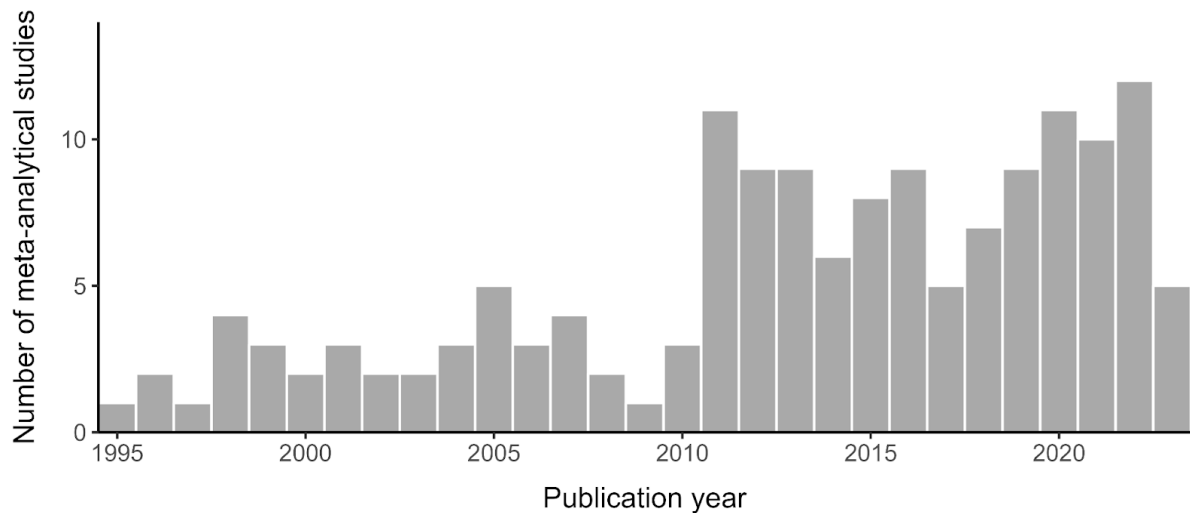
297 Our screening process is summarised in Figure 2. Searches from all sources retrieved a total
298 of 1,215 records, although 397 of them were duplicates. We thus assessed the title, abstract,
299 and keywords of the remaining 818 articles, from which 187 met our initial selection criteria
300 (i.e.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



311

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

313



314

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

318

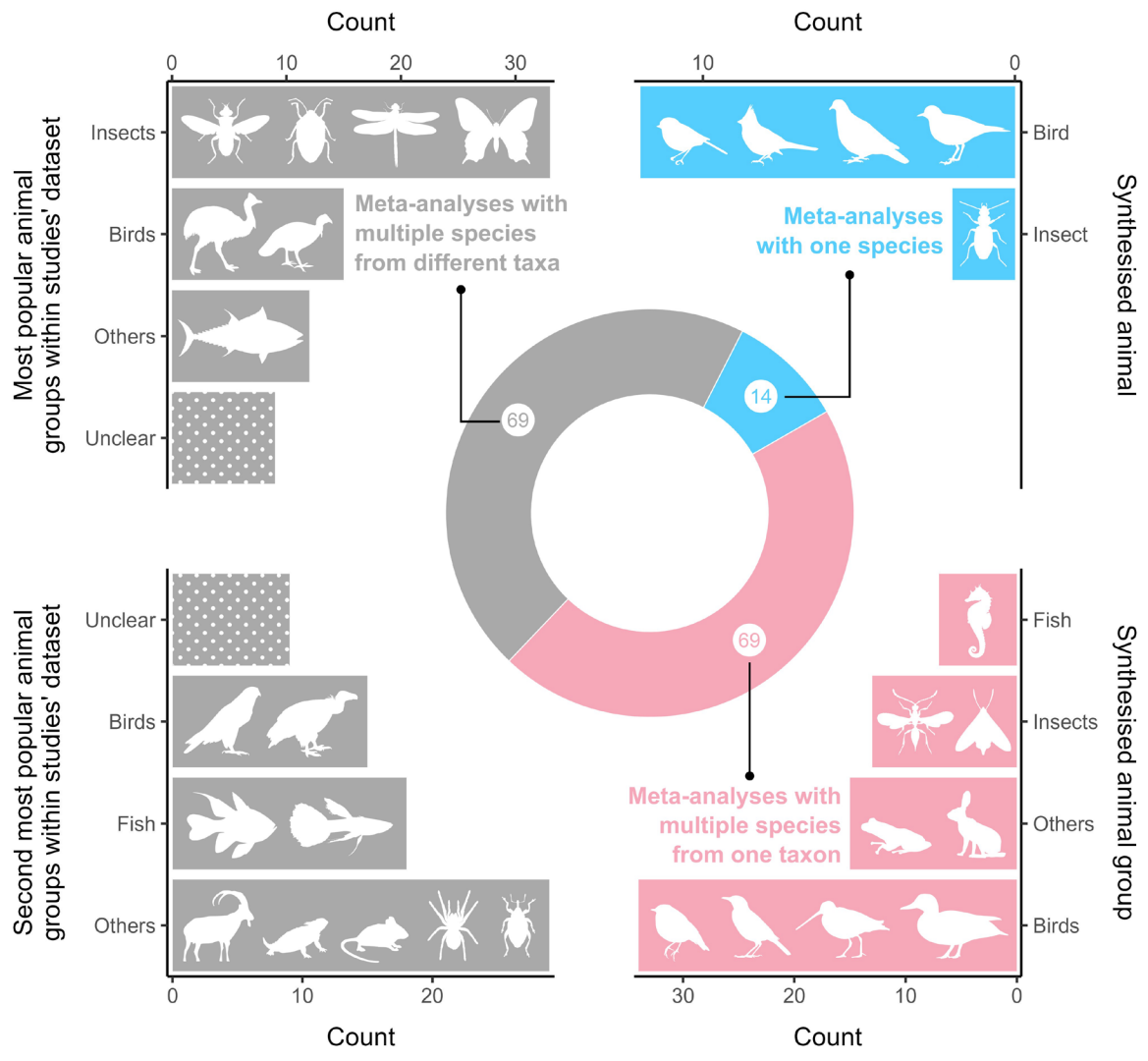
319 *(2) Systematic mapping of meta-analyses on topics related to sexual selection*

320 (a) Taxonomic groups

321 We verified which animal groups (at the taxonomic class level) were synthesised by the
 322 meta-analyses included in our systematic map (Figure 4). We found that more than half of all
 323 of these meta-analyses (83 out of 152; 54.6%) limited their scope to a single species (n = 14)
 324 or to a specific taxonomic group (n = 69), while the remaining ones (n = 69; 45.4% of the
 325 total) did not apply taxonomic filters (i.e. all animal species could be included). We then
 326 identified the animal groups investigated by these meta-analyses, although we could not
 327 obtain relevant details from nine of them (all taxonomically unrestricted meta-analytical
 328 studies). Birds were by far the most popular animal group observed in our systematic map: 12
 329 out of 14 (85.7%) single species meta-analyses focused on a bird species, 34 out of 69
 330 (49.3%) specific taxonomic group meta-analyses focused exclusively on birds, and 30 out of
 331 60 (50%) taxonomically unrestricted meta-analyses for which we obtained taxonomic details

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

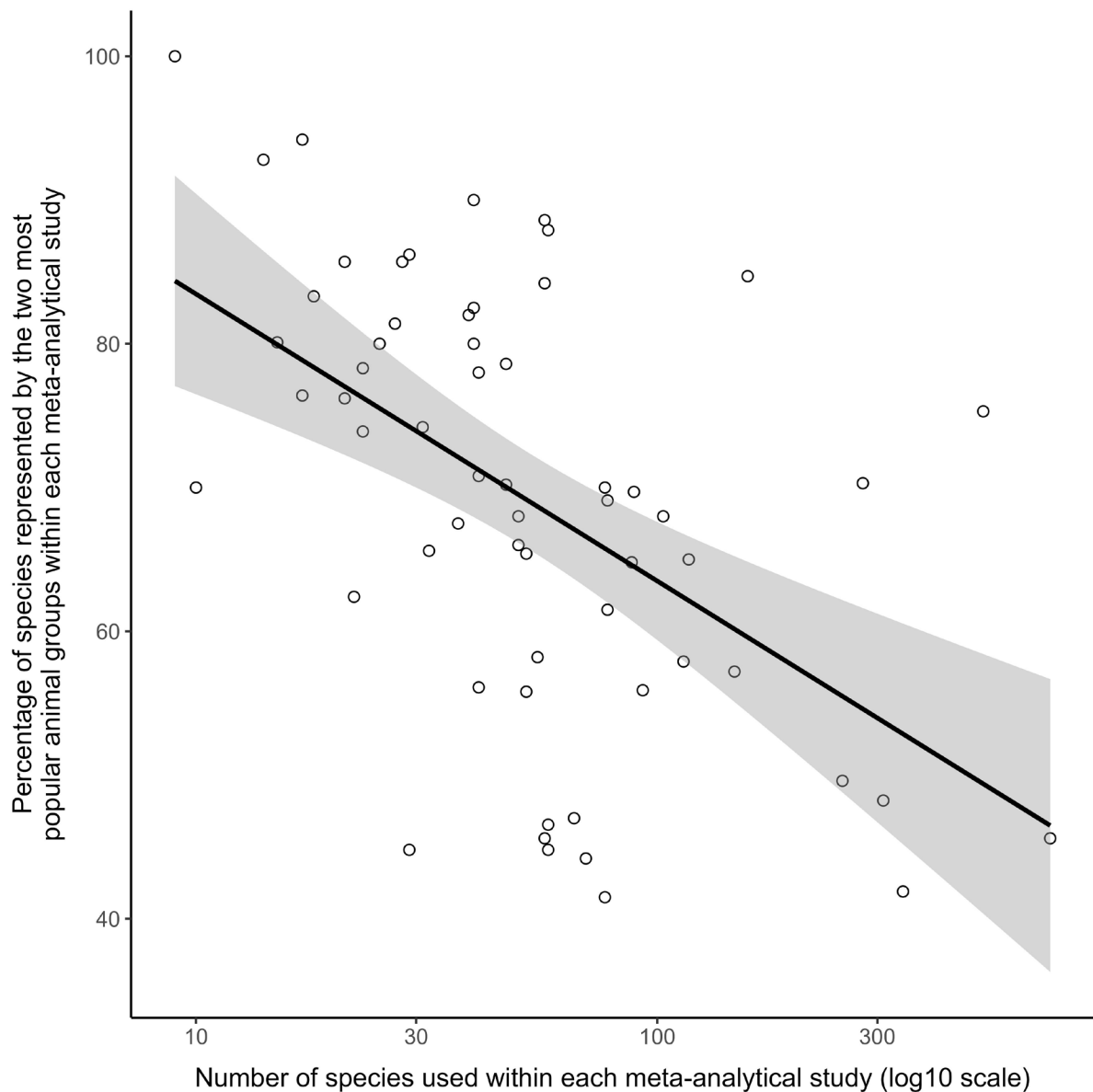
346



347

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

351



352

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

356

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

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

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

381

382 (b) Inclusion of humans

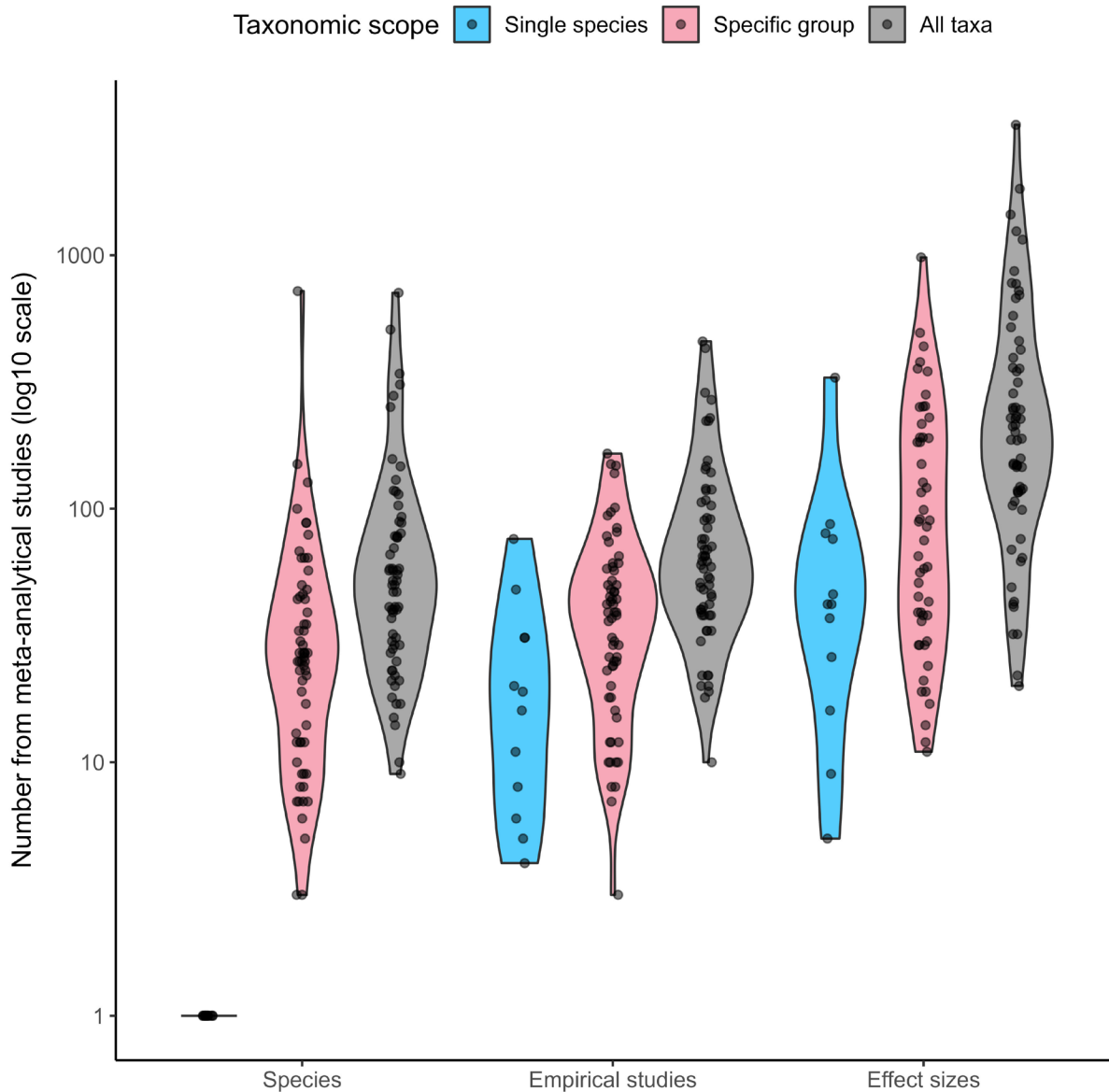
383 Our systematic map deliberately required that meta-analytical studies had to explore non-
384 human animals to be included (see section II.2). Yet, humans could be used along other
385 species in these meta-analyses. We found that 18 studies from our systematic map included

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

392

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

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



412

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

416

417 (d) Study design

418 Briefly stating the design employed by selected empirical studies (experiments or field
419 observations) represents the bare minimum of transparency from meta-analyses. Yet, we

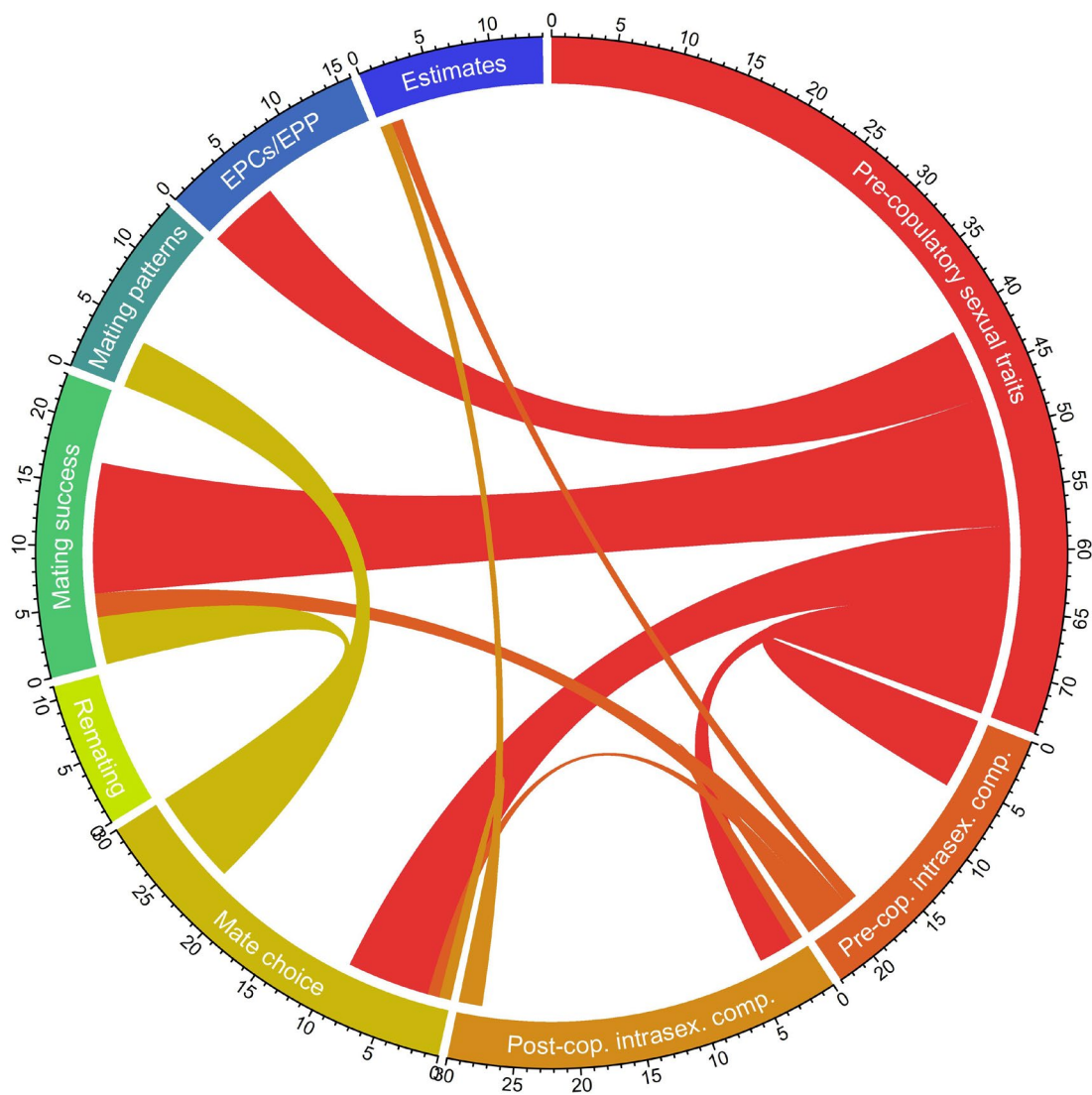
420 found that almost 40% ($n = 60$) of the meta-analytical studies from our systematic map were
421 unclear about this information. From those that specified this information ($n = 92$), 13
422 exclusively used field observations, 32 exclusively used experimental investigations, while
423 47 combined both of these designs. A comprehensive description of included studies'
424 methodology is ideal as it helps meta-analyses' readers to identify some of their limitations
425 (Page *et al.*, 2021). This is because observations and experiments can have multiple
426 peculiarities and vary in the degree of variables controlled, especially when distinct
427 organisms require methodological adjustments. The design type selected by a meta-analysis
428 has direct impacts on what is in fact being evaluated. For instance, to attest mate choice one
429 needs to isolate several variables (e.g. number of individuals present; see section III.5.d), so
430 field observations are much less reliable. Mixing approaches is fine as long as authors use
431 moderators to distinguish one design from another (e.g. mate choice experiments vs. mating
432 success observations), which is another aspect missing in many meta-analyses in the field of
433 sexual selection.

434

435 (e) Overview of topics related to sexual selection

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

445 material). This resulted in 138 questions associated with a single topic and 49 of them
 446 associated with two topics (visualised as links between categories in Figure 7). Details of
 447 what each category within our classification framework encompass are given and discussed
 448 in section III.5.
 449



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

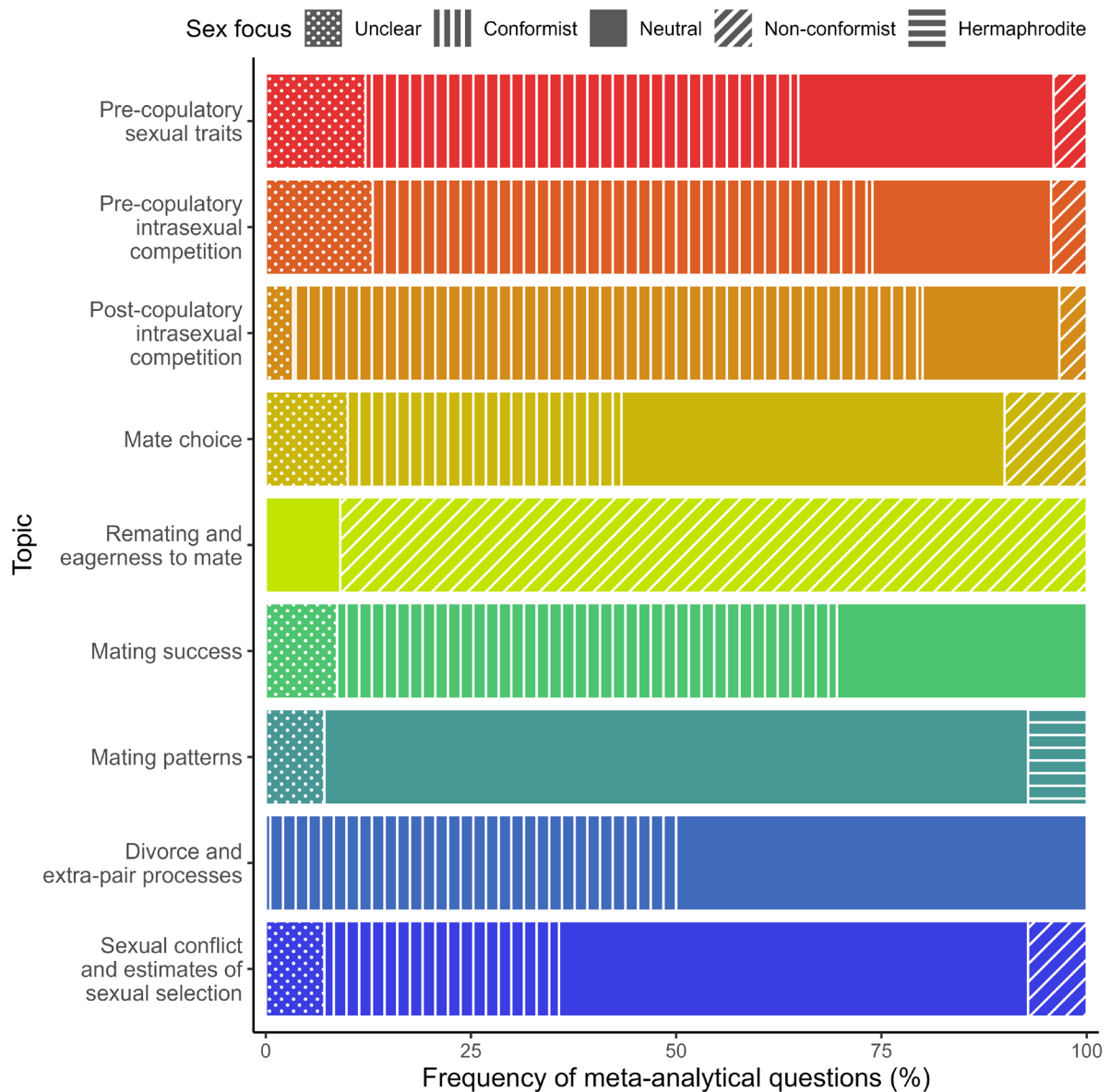
454 copulatory intrasexual competition and associated traits, mate choice, remating and eagerness
455 to mate, mating success, mating patterns, divorce and extra-pair patterns (EPCs/EPP), sexual
456 conflict and estimates of sexual selection.

457

458 (f) Focal sex

459 Our results are summarised in Figure 8, which shows that studies with sex roles conformist
460 (i.e. that focus only on males, except for questions on mate choice) and neutral approaches
461 dominate meta-analyses related to sexual selection. In addition, a single study exclusively
462 focused on hermaphrodite animals (Graham *et al.*, 2015), and 14 studies did not clarify the
463 sex of individuals they focused on for any of their questions. Non-conformist approaches
464 only preponderate over others on questions regarding remating and eagerness to copulate, as
465 studies on this topic essentially tested the benefits and costs of polyandry (see section III.5.e).
466 Conversely, questions on mating patterns are more sex-neutral than others, but this might
467 simply reflect their inherent approach using data from (heterosexual) social pairs or couples
468 in copula. However, we emphasise that questions from other topics that are answered with
469 sex-neutral data might still show a skewed ratio of males and females in their dataset. For
470 example, White (2020) evaluated whether structural colours are associated with individual
471 quality in both sexes, but 146 effect sizes were from males and only 29 were from females.
472 This sex imbalance is quite common in other (not so) sex-neutral meta-analyses from our
473 systematic map, confirming that sex bias is a reality in the field of sexual selection (see also
474 Tang-Martinez, 2016; Pollo & Kasumovic, 2022).

475



476

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

481

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

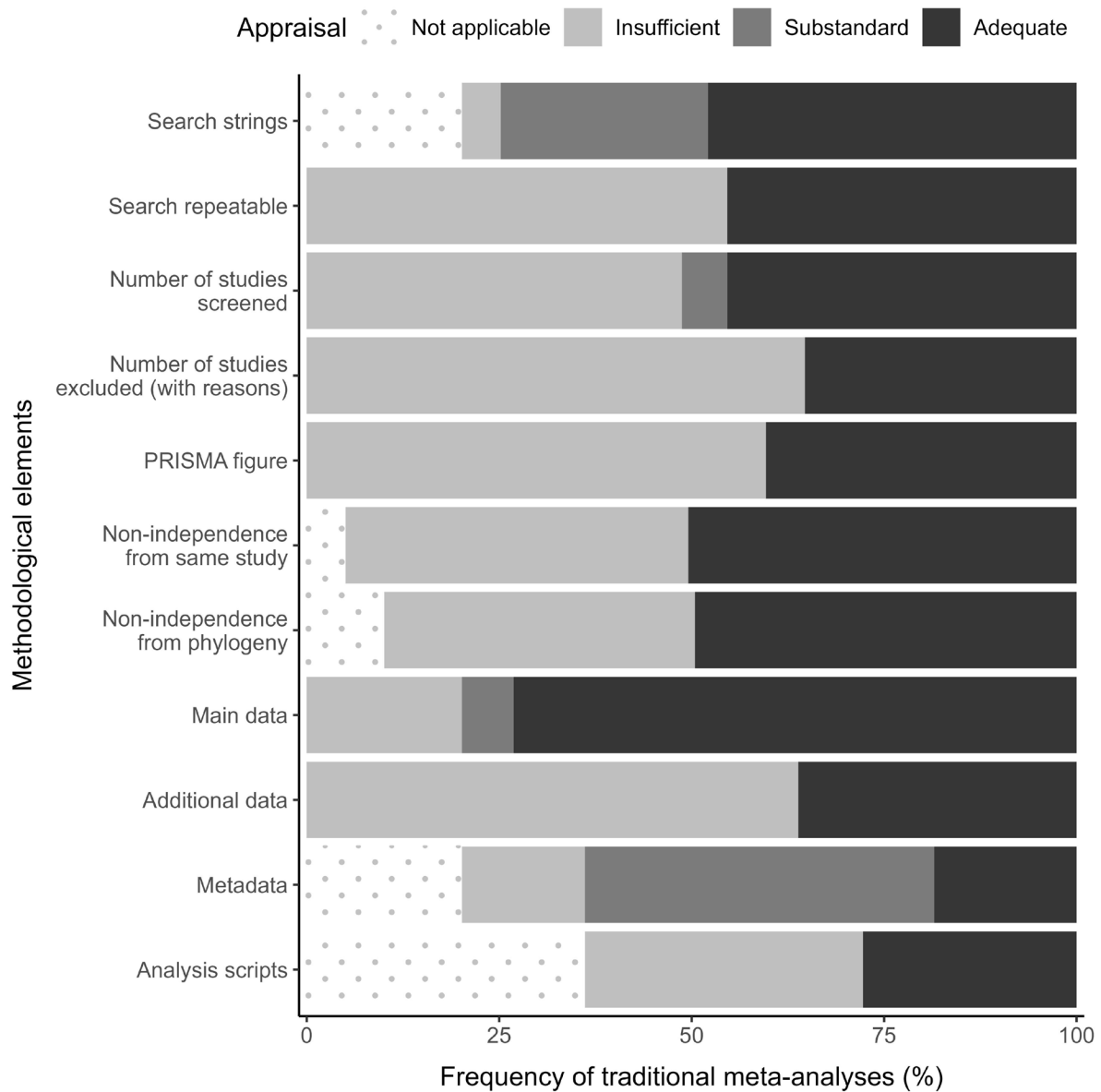
485 Darwin (1859, 1871) started this process: at first, he defined sexual selection as an
486 evolutionary pressure acting exclusively on males, and frequently employed sexual
487 stereotypes in his work. Although since then researchers have advanced our knowledge and
488 perceptions on both sexes, the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

501

502 (3) Reporting appraisal of traditional meta-analyses

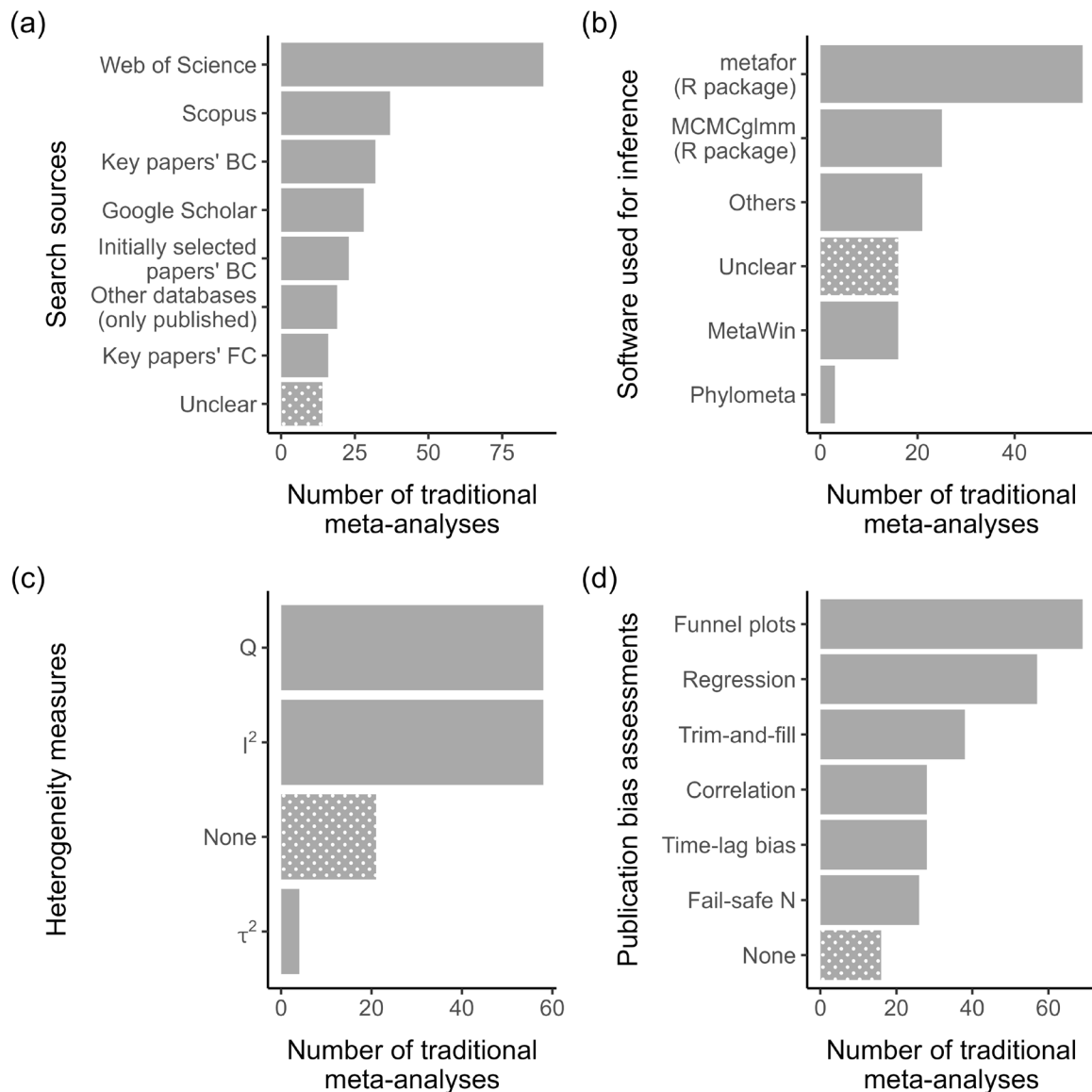
503 Almost 80% (n = 119) of the studies included in our systematic map (i.e. broad sense meta-
504 analyses, see section II.2) were classified as traditional meta-analyses (i.e. used traditional
505 effect sizes and properly modelled heterogeneity using additive weighting rather than
506 multiplicative weighting; see Nakagawa *et al.* (2023a). The rest of the studies (n = 33) used
507 other comparative methods, from simple linear regressions on raw data (e.g. Bailey &
508 Hammond, 2003) to more sophisticated statistical approaches (e.g. Wang *et al.*, 2019 used
509 formal effect sizes and mixed effects models with multiplicative weights where heterogeneity

510 cannot be easily obtained). In this section, we evaluated methodological details only from
 511 traditional meta-analyses, as other comparative studies commonly do not adhere to classic
 512 meta-analytical standards. Figures 9 and 10 summarise results of our appraisal, which are
 513 comparable to other similar studies (e.g. Philibert, Loyce & Makowski, 2012; O’Leary *et al.*,
 514 2016; O’Dea *et al.*, 2021; Nakagawa *et al.*, 2023b; Yang *et al.*, 2023a).
 515



516
 517 Figure 9. Appraisal of traditional meta-analyses on topics associated with sexual selection
 518 regarding several methodological elements. Elements poorly provided or absent were

519 considered insufficient. Substandard appraisal was given to elements that were provided but
 520 with caveats, while adequate appraisal was given to elements competently provided. Certain
 521 elements were not applicable to be judged depending on the meta-analytical study (see details
 522 on section III.3).
 523



524
 525 Figure 10. Details of methodological elements used by traditional meta-analyses on topics
 526 associated with sexual selection. Note that each meta-analysis could utilise multiple search

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

529

530 (a) Searches

531 Meta-analyses should describe their search methods in detail to make the retrieval of the
532 same set of empirical studies by other researchers possible. This first involves describing the
533 exact sources used to conduct searches. However, we found that 12% of the traditional meta-
534 analyses did not provide any information on how authors searched for relevant empirical
535 studies. For meta-analyses included in our systematic map that gave this information, the
536 most popular search sources were databases (e.g. Web of Science, Scopus), followed by
537 backward citations (i.e. reference lists) from relevant key papers or initially selected studies
538 (Figure 10A). These sources usually do not capture grey literature (i.e. unpublished studies).
539 Sources that can capture grey literature (e.g. Google Scholar, BASE, etc) were rarely used in
540 our sample of meta-analyses. Note that every meta-analytical study should use multiple
541 search sources to be comprehensive.

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

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

559

560 (b) Screening process

561 We verified whether traditional meta-analyses provided the number of studies screened in at
562 least two screening phases (i.e. initial and full-text). We considered the associated
563 information provided to be substandard when this number was reported for only one phase or
564 when it was not exact (e.g. Hasik & Siepielski, 2022). This resulted in 49%, 45%, and 6% of
565 traditional meta-analyses from our systematic map showing insufficient, adequate, and
566 substandard information on the number of studies screened, respectively (Figure 9).

567 Meta-analytical studies need to be transparent with their screening decisions,
568 explicitly reporting the number of studies excluded at the full-text screening stage with
569 justifications that clarify each of these exclusions. Thus, we deemed papers that only
570 provided this information for their initial screening phase (e.g. Nolzco *et al.*, 2022) or
571 provided a list of exclusion reasons and the total number of excluded papers (instead of
572 exclusion reason for each paper, e.g. Weaver *et al.*, 2018) as insufficient information. This
573 culminated in only 35% of traditional meta-analyses properly describing the justification for
574 their full-text excluded papers (Figure 9).

575 Both the number of studies screened and excluded (with justifications) should ideally
576 be presented in a PRISMA-like diagram, which summarises both the search and screening

577 processes (O’Dea *et al.*, 2021). A few papers presented figures that lacked too many
578 necessary diagram elements, so we considered them insufficient (e.g. Harts, Booksmythe &
579 Jennions, 2016; Hasik & Siepielski, 2022). We found that only 40% of the traditional meta-
580 analyses from our dataset showed adequate PRISMA-like diagrams (Figure 9).

581

582 (c) Software and data non-independence

583 Some traditional meta-analyses related to sexual selection did not describe the software used
584 for analysis (n = 16; although some papers might have not used any, e.g. manual
585 calculations), while others used stand-alone software (e.g. MetaWin, Phylometa, etc). On the
586 other hand, most meta-analyses used the R packages *metafor* (Viechtbauer, 2010) and/or
587 *MCMCglmm* to make inferences (Hadfield, 2010) (Figure 10B), which are the most
588 appropriate meta-analytical tools as they can incorporate phylogeny and other types of non-
589 independence. We emphasise that some meta-analyses used more than one software for the
590 same question and dataset to strengthen their results (e.g. Goldberg *et al.*, 2020).

591 Non-independence among effect sizes often occurs in meta-analyses, which can lead
592 to false conclusions if not properly addressed (Noble *et al.*, 2017; Cinar, Nakagawa &
593 Viechtbauer, 2022). We specifically examined whether traditional meta-analyses from our
594 dataset dealt with non-independence from shared study identities (i.e. when at least two effect
595 sizes are extracted from the same study) and from phylogenetic relatedness. We found that
596 approximately half of the meta-analytical studies evaluated dealt with at least one of these
597 non-independence sources (Figure 9), usually through random factors in meta-analytical
598 models. We emphasise that non-independence might be entirely absent (i.e. not applicable;
599 Figure 9) from meta-analyses whose effect sizes are all extracted from different studies (i.e.
600 independent) or when they investigate only a single species (see section III.2.a).

601

602 (d) Sharing of data, metadata, additional data, and analysis scripts

603 Lack of data transparency is a major obstacle for reproducibility (Wilkinson *et al.*, 2016;
604 Munafò *et al.*, 2017). First, meta-analyses need to provide data with effect size values and all
605 other variables used in their analyses (e.g. moderators). We refer to these datasets as main
606 data, as studies can also provide additional data (e.g. raw measurements or location from
607 which they were extracted in empirical papers). We found that 73% and 7% of traditional
608 meta-analyses on topics related to sexual selection provided all or some (i.e. substandard) of
609 their main data, respectively (Figure 9). These findings are a little more optimistic than those
610 found by a survey of the primary literature in ecology and evolution (Roche *et al.*, 2015),
611 although metadata quality was used to assess data completeness and reusability in it (which
612 we do separately below). However, we note that many datasets were simply given as tables
613 in-text (rather than separate files), which makes it more difficult to re-use them in future
614 studies. In addition, data were supposedly provided but could not be accessed in some cases
615 (e.g. due to broken links; Guindre-Parker & Love, 2014; Dougherty, 2023), emphasising that
616 authors must ensure that any resources mentioned in their papers are truly available to
617 readers. Furthermore, despite main data being shared in most meta-analytical studies, only
618 36% of meta-analyses evaluated provided additional data (Figure 9), highlighting another
619 obstacle for reproducibility.

620 Providing data is crucial, but this might be useless if data are incomprehensible
621 (Roche *et al.*, 2015). The optimal option to avoid this issue consists in providing a separate
622 file with metadata (i.e. information that fully describes all fields from the main dataset
623 provided), which occurred in only 18% of traditional meta-analyses evaluated by us (Figure
624 9). Nonetheless, another 45% of the studies showed easily understandable data (e.g. from the
625 study context, no acronyms used) and, even though we considered these cases as substandard
626 for lacking proper metadata (Figure 9), these resources were occasionally clear and

627 informative (e.g. tables in Meunier *et al.*, 2011; Graham *et al.*, 2015). We also note that
628 metadata were not applicable for traditional meta-analyses that did not provide any of their
629 main data (ca. 20%).

630 At last, sharing analysis scripts is essential for others to reproduce meta-analytical
631 findings (Piccolo & Frampton, 2016; Culina *et al.*, 2020). This, however, may not apply to
632 traditional meta-analyses from our dataset that used point-and-click software ($n = 27$) or that
633 did not specify the software they used for inferences ($N = 16$). Therefore, we found that only
634 28% of the studies evaluated in our appraisal appropriately shared their code (Figure 9),
635 which is similar to findings from recent reports on code availability in ecology (Culina *et al.*,
636 2020). This can be a result of lack of incentives for authors to share their code (see Gomes *et*
637 *al.*, 2022) or lack of the awareness of the importance of software in research.

638

639 (e) Heterogeneity and publication bias

640 Heterogeneity measures the amount of variation among effect sizes, thus being critical to
641 understanding the generality of overall effect sizes shown in meta-analytical studies (Spake *et*
642 *al.*, 2022); see section III.6). We found that only 18% of traditional meta-analyses did not
643 calculate any heterogeneity measure. Those that did most frequently used Q and/or I^2 (Figure
644 10C). We note that H^2 (Lynch, 1991) or Pagel's λ were commonly present in phylogenetic
645 regressions, which we did not consider proper heterogeneity measures for a meta-analysis.

646 Meta-analytical studies also must investigate publication bias in their included
647 dataset, as this can drastically impact results' magnitude and sign errors (Yang *et al.*, 2023b).
648 87% of traditional meta-analyses from our dataset assessed publication bias in some way.
649 Funnel plots were the popular tool to address publication bias (Figure 10D), similar to
650 Nakagawa *et al.* (2021) findings.

651

652 (f) Other elements

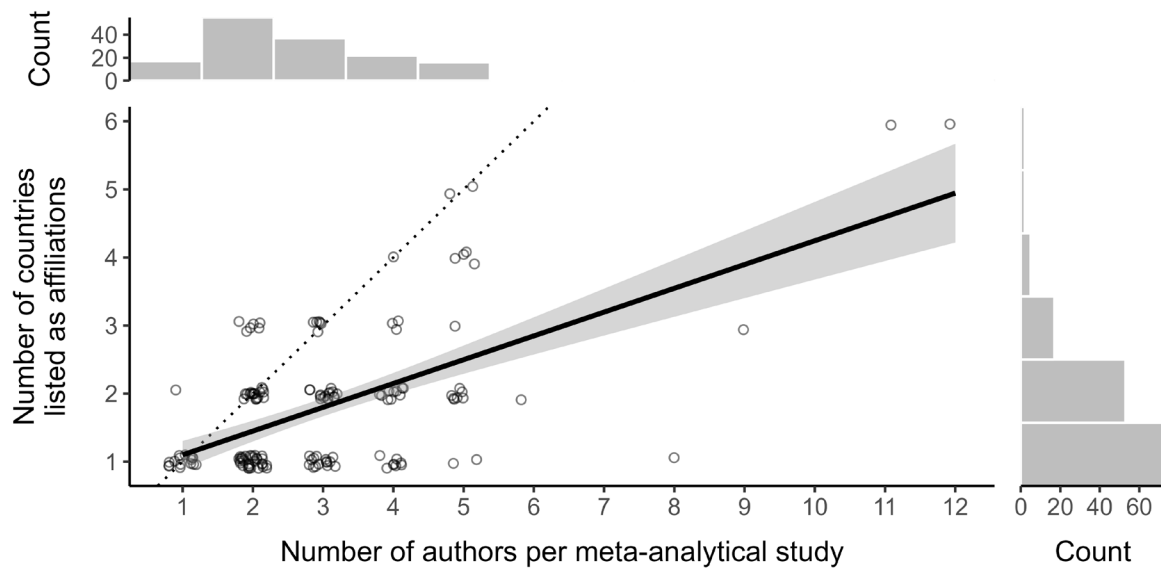
653 We verified the occurrence of several other important methodological elements in traditional
654 meta-analyses, but rarely found them. For instance, only one study was pre-registered (e.g.
655 Kim *et al.*, 2021) and none mentioned post-hoc hypotheses (although there were cases of
656 post-hoc analyses;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

667

668 *(4) Bibliometric analysis*

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

676



677

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

683

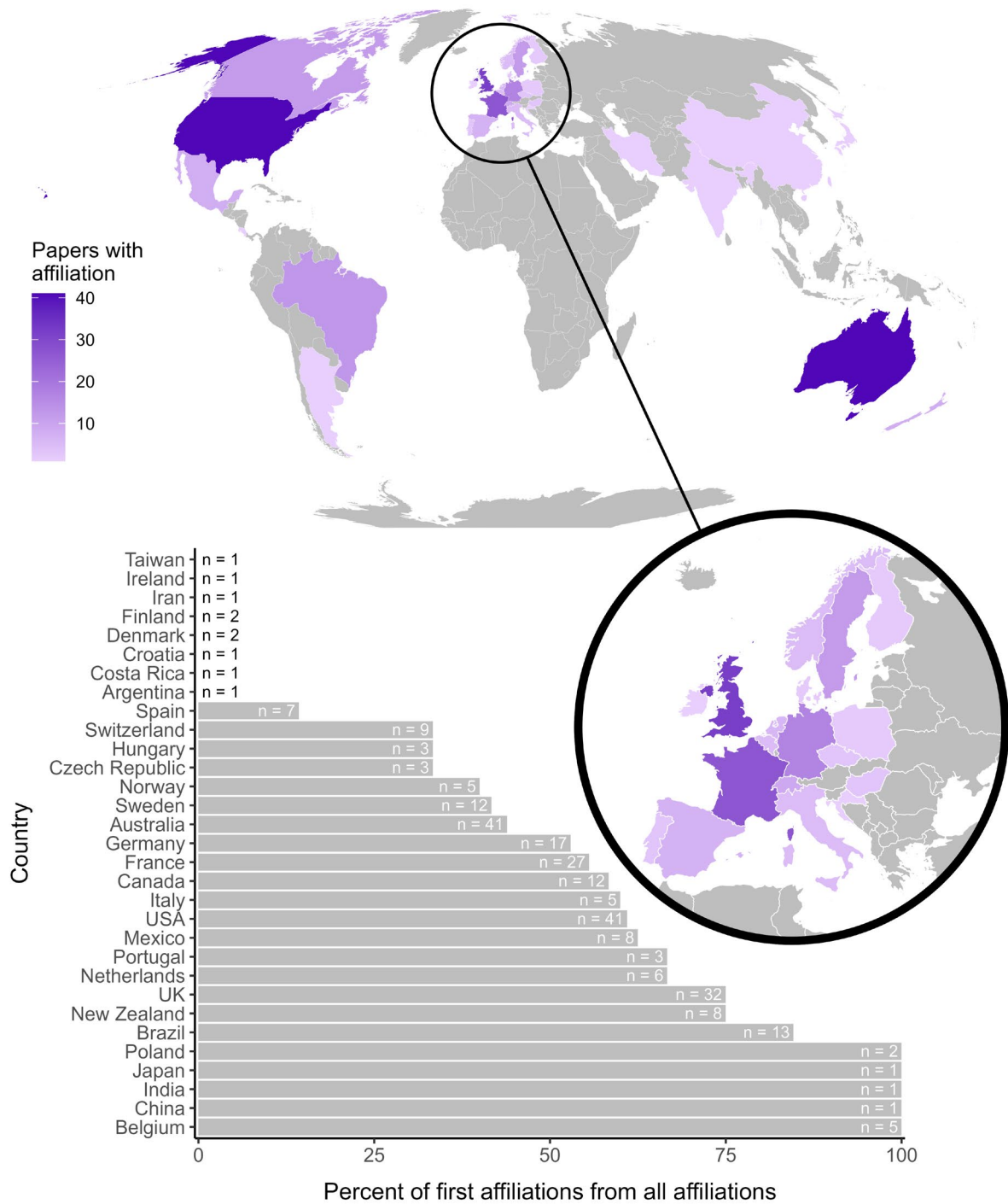
684 (a) Authors' affiliations

685 Australia and the United States of America (hereby USA) were the most prolific countries
 686 regarding meta-analyses on topics associated with sexual selection, each with 41 studies from
 687 our dataset being authored by at least one researcher affiliated to an institution located there
 688 (Figure 12). We detected only a few developing countries (i.e. Global South) as affiliations in
 689 the evaluated meta-analyses. In fact, the only countries with more than a single study
 690 affiliated outside of Anglo-America, Europe, or Oceania, were Brazil and Mexico (Figure
 691 12).

692 The first affiliation listed in each study, which is usually associated with the lead authorship,
 693 revealed a similar authorship pattern. The USA also led the highest number ($n = 25$) of

694 studies with one of its institutions as the first affiliation listed in papers, albeit the United
695 Kingdom followed close behind with 24 first affiliations. The proportion of first affiliations
696 to all affiliations seen per country can serve as a proxy of how dependent a country is on
697 international collaborations (Figure 12). For example, despite seven meta-analytical studies
698 being associated with an institution from Spain, only in one of them a Spanish institution was
699 the first affiliation listed. In contrast, Belgian institutions were first listed as affiliations in all
700 of five meta-analyses associated with Belgium. We emphasise, however, that this proportion
701 tends to extreme values (i.e. none or all) with fewer studies associated with a country (Figure
702 12). Furthermore, we note that almost half of all meta-analyses evaluated ($n = 73$) were
703 affiliated to a single country (Figure 12).

704



705

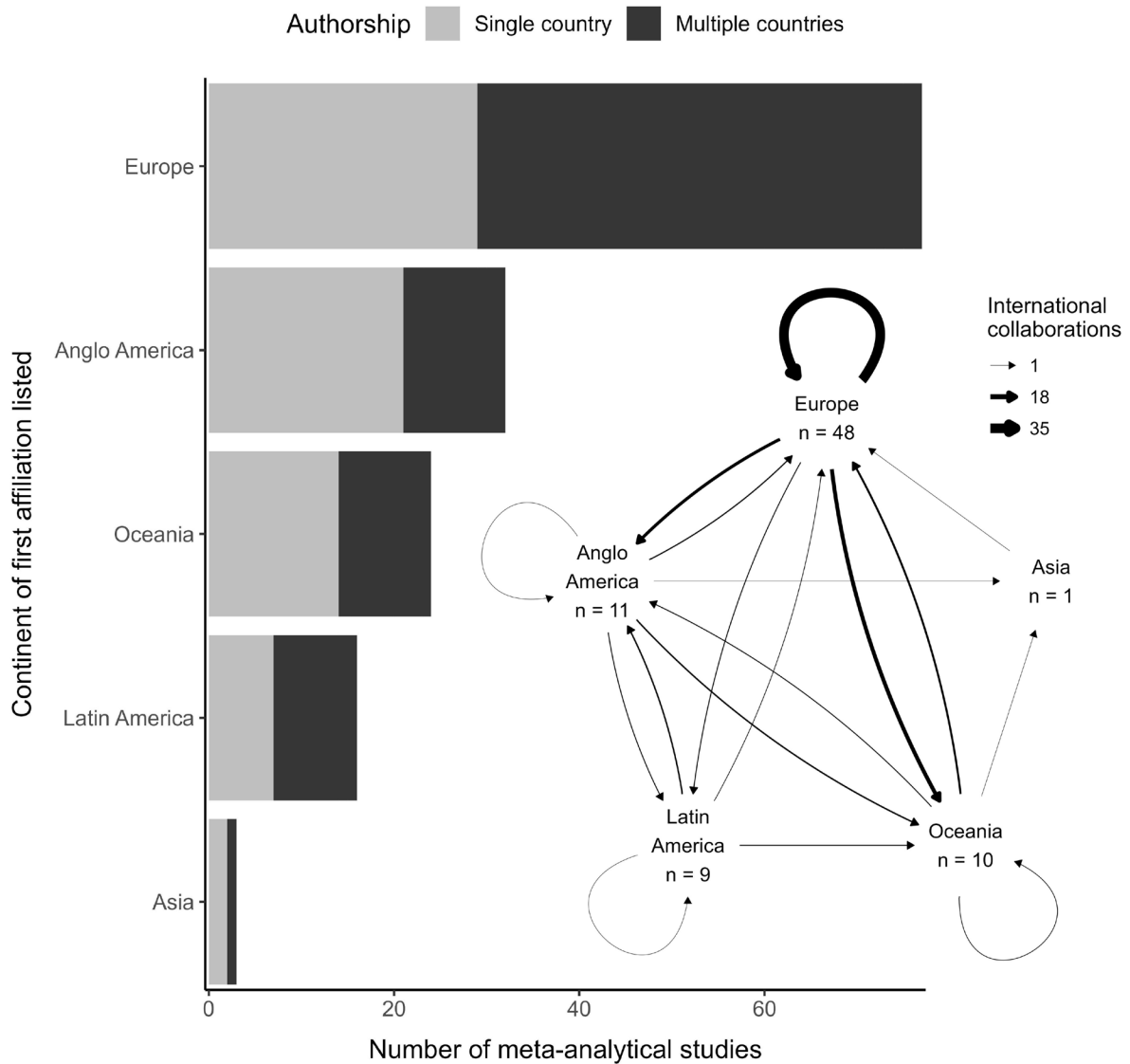
706 Figure 12. Affiliations reported in meta-analytical studies on topics associated with sexual
 707 selection. Colour intensity in maps (top and inset) illustrate the number of papers in which
 708 countries' institutions were recorded as authors' affiliations, greyed countries representing
 709 zero.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

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

712

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

722



723

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

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

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

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

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

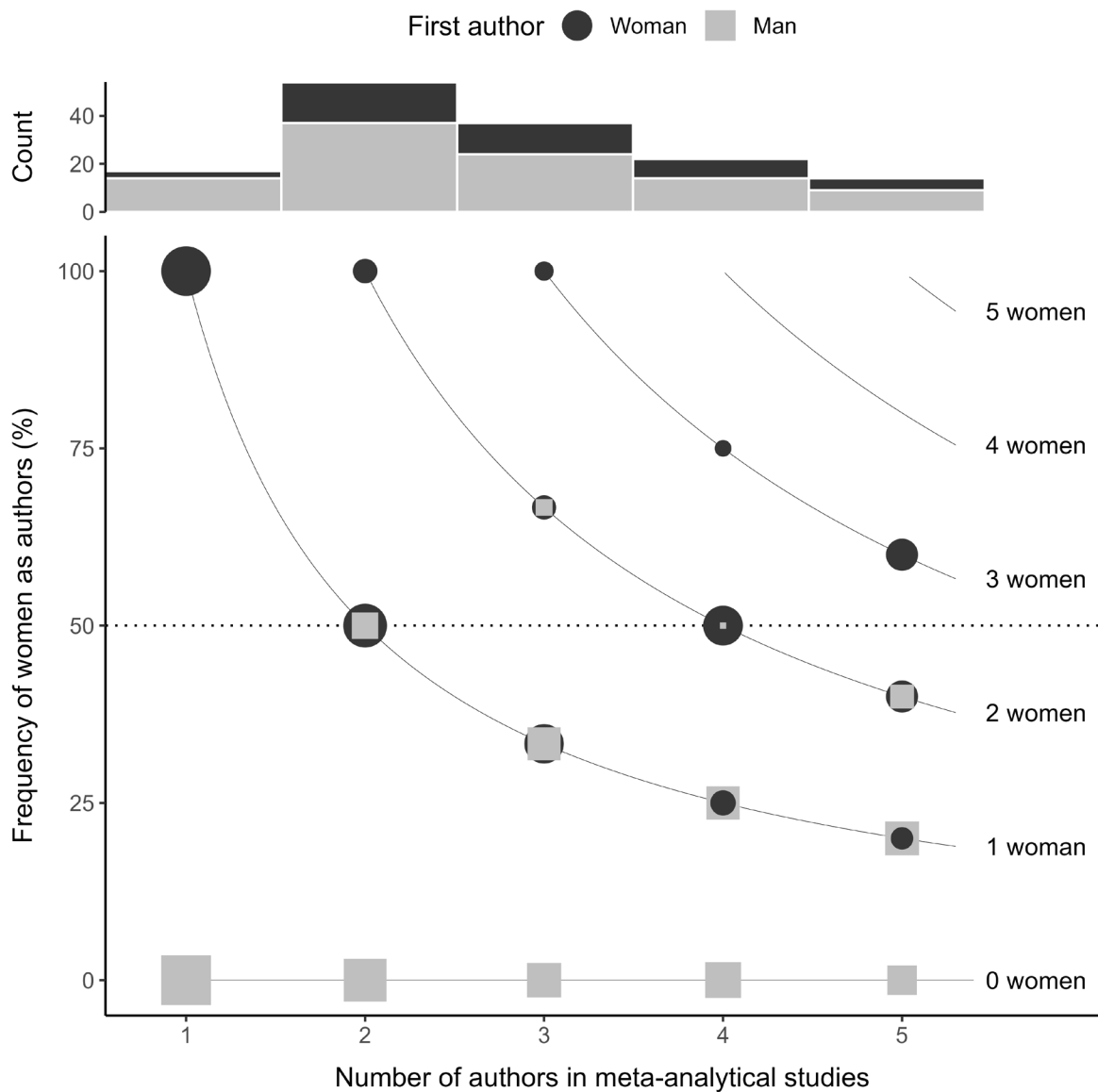
729

730 (b) Authors' gender

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

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

733 identified as men (n = 199; gender could not be assigned to the remaining 2% of authors).
 734 This gender disparity increased when considering only first authors, as 68% of them were
 735 identified as men and 31% as women (1% was unknown). The number of women in multi-
 736 authored studies was rarely greater than the number of men, even when women were first
 737 authors (Figure 14). On the other hand, men predominated in research projects led by them.
 738 In fact, we detected only three studies led by men with a greater number of women than men
 739 as participating authors (Figure 14).
 740



741

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

747

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

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

759

760 (a) Pre-copulatory sexual traits

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

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

770 The emphasis on pre-copulatory sexual traits is expected, as Darwin (1871) himself
771 used them to develop the theory of sexual selection (see section III.6.b). He proposed that
772 ornaments and sexual signals evolved via mate choice, an idea that was rejected by his peers
773 at the time (Hoquet & Lewandowsky, 2015). Nonetheless, the literature on ornaments and
774 sexual signals later flourished when a debate among evolutionary biologists was established:
775 whether these traits and signals evolved because they reflect greater genetic quality to
776 prospective mates (“good genes” model and its “handicap principle” extension; Zahavi, 1975,
777 1977) or simply because they genetically correlate with mate preference for themselves (i.e.
778 Fisherian runaway process; Fisher, 1930; see also Eshel, Volovik & Sansone, 2000; Kokko,
779 2001; Hoquet & Lewandowsky, 2015). Possibly because the latter is complex and difficult to
780 measure (but see Greenfield *et al.*, 2014), the former has received much more empirical
781 attention.

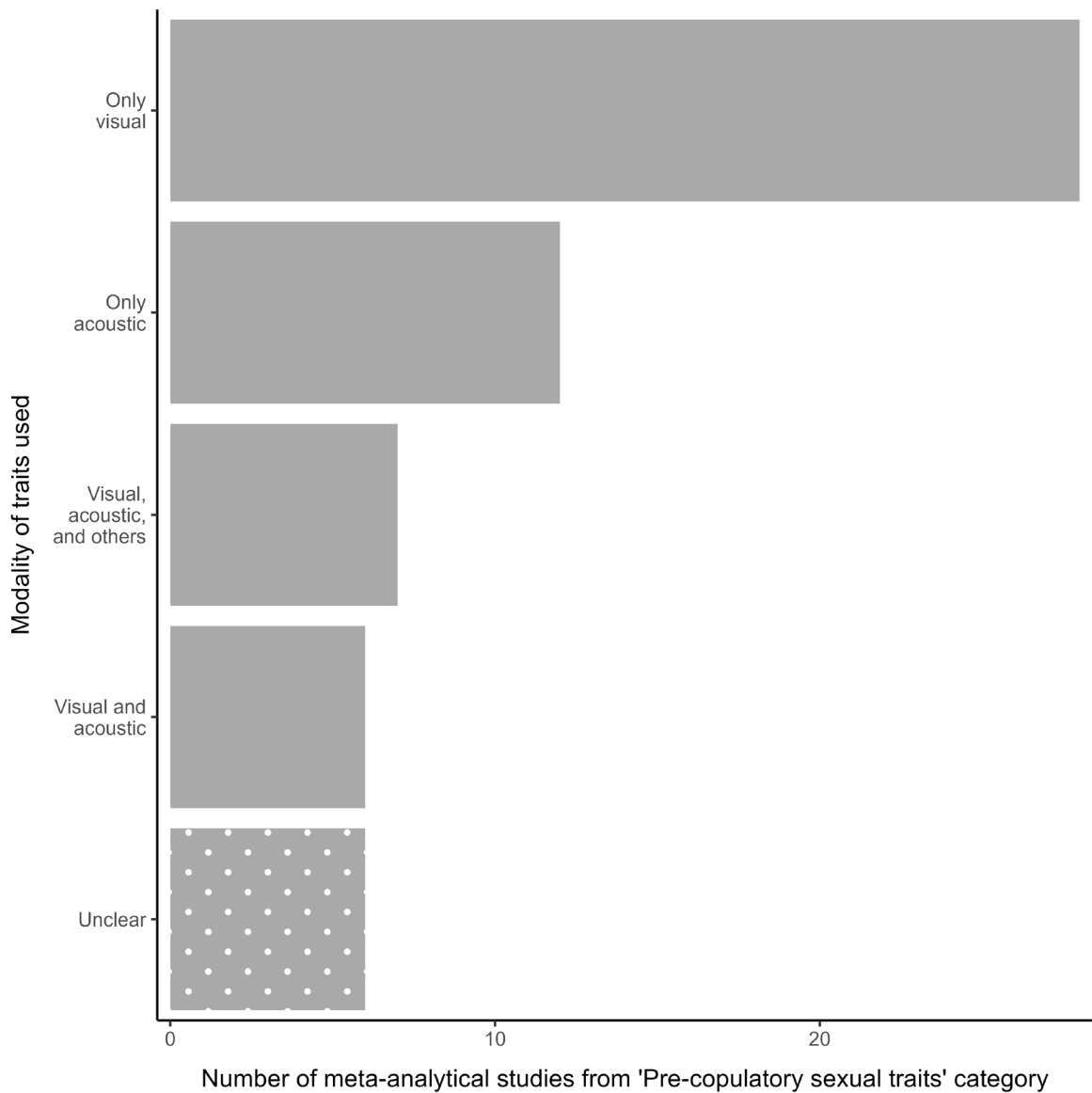
782 On one hand, some proponents of the good genes model (e.g. Andersson, 1994)
783 predicted that ornaments and sexual signals would be linked to fitness-impacting measures
784 (e.g. survival, fecundity, viability, overall reproductive success; see Kokko, 2001), which was
785 tested by many different meta-analyses (Table S5). On the other hand, Grafen (1990a, 1990b)
786 popularised Zahavi’s (1975, 1977) idea that ornaments and sexual signals must be condition-
787 dependent to be honest (reviewed and contested in Penn & Számadó, 2020; see also Getty,
788 2006), shifting the attention of the research community to more direct questions. It is
789 unsurprising then that 26 meta-analyses in our systematic map contain at least one question
790 asking whether the expression of ornaments and sexual signals are related to the expression
791 of other traits (e.g. age, body size) or to proxies of individual quality (e.g. parasite load; or

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

795 Conversely, a variety of meta-analytical studies ($n = 18$) tested whether certain
796 ornaments and sexual signals might be in fact under selection by verifying their relationship
797 with intrasexual competition (e.g. dominance rank or aggression; Nakagawa *et al.*, 2007;
798 Yasukawa *et al.*, 2010; Santos, Scheck & Nakagawa, 2011; Parker, 2013; Sánchez-Tójar *et*
799 *al.*, 2018), species recognition (Ord & Stamps, 2009; Ord, King & Young, 2011; Parker *et*
800 *al.*, 2018), attractiveness in mate choice experiments (Parker & Ligon, 2003; Simons &
801 Verhulst, 2011; Hernández *et al.*, 2021), mating success, or extra-pair patterns (see in Table
802 S5). Other meta-analytical studies explored whether courtship behaviours, ornaments, and/or
803 sexual signals are related to specific biotic (e.g. density, predation, etc; Weir, Grant &
804 Hutchings, 2011; De Jong *et al.*, 2012; Dougherty, 2021a; White, Latty & Umbers, 2022) and
805 abiotic conditions (e.g. habitat structure, band colouration, etc; Boncoraglio & Saino, 2007;
806 Seguin & Forstmeier, 2012; Parris & McCarthy, 2013). At last, other specific meta-analytic
807 studies assessed sexual traits' additive genetic variation (Pomiankowski & Møller, 1995) and
808 heritability (Prokop *et al.*, 2012; Prokuda & Roff, 2014), compared the allometry of sexual
809 traits depending on their function and denomination (Voje, 2016; Rodríguez & Eberhard,
810 2019), verified whether pre-copulatory sexual traits are associated with sperm quality (Mautz,
811 Møller & Jennions, 2013), examined the interplay between call length and reply latency
812 across species (Bailey & Hammond, 2003), and evaluated the association between expression
813 of possibly sexually selected traits and speciation rates (Kraaijeveld, Kraaijeveld-Smit &
814 Maan, 2011).

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

817 addition, some studies were unclear on the exact traits used (see also section III.6.b). We
818 observed only seven meta-analytical studies with a question focusing on pre-copulatory
819 sexual traits from other modalities (Figure 15; Table S6). Yet, even in these studies, visual
820 and acoustic traits predominate over others, revealing that some sensory modalities (e.g.
821 olfactory) are neglected. We discuss the implications of this pattern in section III.6.b.
822



823

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

827

828 (b) Pre-copulatory intrasexual competition and associated traits

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

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

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

853 As previously mentioned, some studies evaluated whether ornaments are linked to
854 aggression or dominance (Nakagawa *et al.*, 2007; Yasukawa *et al.*, 2010; Santos *et al.*, 2011;
855 Parker, 2013; Sánchez-Tójar *et al.*, 2018). In respect to territoriality, Ord (2021) assessed the
856 costs associated with this behaviour whilst (Ord *et al.*, 2011) verified whether species
857 recognition occurs for territorial signals. Other meta-analytical investigations explored
858 whether different contexts and conditions are associated with the expression and intensity of
859 intrasexual competition, such as operational sex ratio (Weir *et al.*, 2011), environmental
860 stability (Peixoto, Medina & Mendoza-Cuenca, 2014), and availability of reproductive sites
861 (Alissa, 2018). Finally, certain meta-analyses attempted to answer questions involving other
862 topics by examining the following relationships: mating success and fighting frequency
863 (Fiske, Rintamaki & Karvonen, 1998) or social dominance (Majolo *et al.*, 2012), strength of
864 mate choice and traits determinant to intrasexual competition success or attractiveness (Pollo
865 *et al.*, 2022), and mate monopolisation and estimates of sexual selection (Macedo-Rego *et al.*,
866 2020b) or the effect of body size on reproductive success (Macedo-Rego *et al.*, 2020c).

867

868 (c) Post-copulatory intrasexual competition and associated traits

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

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

877 Most questions in this category concentrated on the expression of gametes, ejaculates,
878 and/or primary sexual traits. For example, several meta-analyses investigated the relationship
879 between these traits, their allocation, or their production, and either (1) another type of trait
880 (e.g. alternative reproductive tactics: Aguiar Del Matto, 2018; Dougherty *et al.*, 2022; body
881 size or mass: Hayward & Gillooly, 2011; Lüpold & Fitzpatrick, 2015; Kim *et al.*, 2021;
882 mating status: Zhang *et al.*, 2016; secondary sexual traits: Mautz *et al.*, 2013; weapons:
883 Lüpold *et al.*, 2015), (2) a specific context (e.g. contaminants: Marmol, 2022; diet or nutrient
884 intake: Crean & Senior, 2019; Macartney *et al.*, 2019; inbreeding: Losdat, Chang & Reid,
885 2014; masculinization: Senior, Johnson & Nakagawa, 2016b; mate quality: Kelly & Jennions,
886 2011; presence of ovarian fluid: Myers *et al.*, 2020; presence of rivals: delBarco-Trillo, 2011;
887 Kelly & Jennions, 2011; sexual cannibalism: Dharmarathne & Herberstein, 2022;
888 temperature: García-Roa *et al.*, 2020), or (3) a potential consequence (e.g. allometry patterns:
889 Voje, 2016; patterns of sperm competition risk: Lüpold *et al.*, 2020; trait selection: Dougherty
890 & Shuker, 2016; speciation rates: Kraaijeveld *et al.*, 2011). In addition, some studies
891 evaluated the relationship between two gamete traits (e.g. Bernasconi & Hellriegel, 2005) or
892 between a gamete trait and a primary sexual trait (especially gonad mass; e.g. Joly &
893 Schiffer, 2010; Lüpold & Fitzpatrick, 2015; Lüpold *et al.*, 2015). The remaining questions
894 that fit this category explored the connection between mate guarding and operational sex ratio
895 (Weir *et al.*, 2011), individual quality, or paternity (Harts *et al.*, 2016); copula duration and
896 sperm transfer (Dharmarathne & Herberstein, 2022) or operational sex ratio (Weir *et al.*,
897 2011); and diverse measures of sperm competition and availability of reproductive sites
898 (Alissa, 2018).

899

900 (d) Mate choice

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

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

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

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

944

945 (e) Remating and eagerness to mate

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

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

955 The majority of the questions from this topic are alike: they evaluate the benefits
956 and/or costs to individuals (or to their offspring) of mating multiple times versus mating once
957 or fewer times (Table S5). Similarly, two other studies verified whether individuals' mating
958 history can influence the available resources they have for further copulas, as well as their
959 subsequent impact on the reproductive success of individuals they copulate with (Torres-Vila
960 & Jennions, 2005; Zhang *et al.*, 2016), which ultimately could influence remating decisions.
961 The remaining studies in this category are slightly distinct: Mori & Evenden (2013)
962 investigated the association between delayed mating and fitness, while Pilakouta & Baillet
963 (2022) assessed whether eagerness to mate is related to temperature.

964

965 (f) Mating success

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

974 been discussed in previous topics (see above). Other questions in this category explore
975 whether mating success is linked to body size (e.g. Sokolovska, Rowe & Johansson, 2000;
976 Kim *et al.*, 2021) or to specific conditions (e.g. density and sex ratio: Nieberding & Holveck,
977 2017; lek size: Isvaran & Ponkshe, 2013; parasitism: Hasik & Siepielski, 2022; temperature:
978 Pilakouta & Baillet, 2022).

979

980 (g) Mating patterns

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

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

999 bias (Wang *et al.*, 2019) and sample pooling methods (Rios Moura *et al.*, 2021) were
1000 associated with estimates observed. Lastly, Janicke *et al.* (2019) verified whether assortative
1001 mating is related to species richness.

1002

1003 (h) Divorce and extra-pair patterns

1004 All topics discussed so far are relevant for the entire animal kingdom (although taxa are
1005 unequally investigated, see section III.2.a). Here, however, we discuss divorce, extra-pair
1006 copulations (hereby EPCs), and extra-pair paternity (hereby EPP), which pertain to a specific
1007 niche in the sexual selection literature that applies only to socially monogamous animals
1008 (forming exclusive social pairs for reproduction). In this context, divorce means re-pairing
1009 with another individual whilst the previous partner is still alive (Choudhury, 1995), whereas
1010 EPP refers to fertilizations from EPCs (i.e. copulas outside of the social bond; Griffith,
1011 Owens & Thuman, 2002). Altogether, this category gathered 16 questions from 16 meta-
1012 analyses (Figure 7).

1013 Only three meta-analytical questions involved divorce, verifying the association
1014 between this behaviour with breeding failure before and/or after its occurrence (Dubois &
1015 Cézilly, 2002; Culina *et al.*, 2015; Culina & Brouwer, 2022). Other questions in this category
1016 explored the relationship between EPCs or EPP and certain traits, such as age (Cleasby &
1017 Nakagawa, 2012), ornaments or sexual signals (Table S5), parental care (Arnqvist &
1018 Kirkpatrick, 2005; Albrecht, Kreisinger & Piálek, 2006), pair relatedness (Arct, Drobnik &
1019 Cichoń, 2015; Hsu *et al.*, 2015), or a mix of these traits (Møller & Ninni, 1998; Akçay &
1020 Roughgarden, 2007). In addition, a couple of these studies also tested whether offspring
1021 fitness is associated with its genetic origin (intra- vs extra-pair; Arnqvist & Kirkpatrick, 2005;
1022 Akçay & Roughgarden, 2007).

1023

1024 (i) Sexual conflict and estimates of sexual selection

1025 Here, we briefly review the 14 meta-analytical questions (each from a different study) that
1026 focused on the two remaining topics related to sexual selection: sexual selection estimates
1027 (see Fitze & le Galliard, 2011; Henshaw, Kahn & Fritzsche, 2016; Anthes *et al.*, 2017) and
1028 interlocus sexual conflict (Parker, 1979; Chapman *et al.*, 2003) (Figure 7).

1029 Two meta-analytical studies explored sexual selection on traits using standardised
1030 selection gradients (β : regression between standardised trait values and relative fitness, Lande
1031 & Arnold, 1983). As a fitness proxy, Hoekstra *et al.* (2001) used mating success, whilst
1032 Dougherty & Shuker (2016) used both mating and insemination success. Other estimates of
1033 sexual selection, such as Bateman's gradient (β_{ss} : average reproductive success gains from
1034 each additional mating; Bateman, 1948) and opportunity of sexual selection (I_s or I_{mates} :
1035 variance in relative mating success; Wade, 1979; Shuster & Wade, 2003), were much more
1036 common in our dataset (Table S5). Macedo-Rego *et al.* (2020a, 2020b) also used the Jones'
1037 index (s'_{max} ; Jones, 2009), albeit Rios Moura & Peixoto (2013) made their own estimate (I_{dir} :
1038 I_s if mating were random minus observed I_s). Aside from verifying the mean estimates of
1039 sexual selection found in the literature, several meta-analyses investigated whether these
1040 estimates were associated with other variables, like availability of reproductive sites (Alissa,
1041 2018), monopolisation of mates (Macedo-Rego *et al.*, 2020b), operational sex ratio (Rios
1042 Moura & Peixoto, 2013; Janicke & Morrow, 2018), sexual size dimorphism (Janicke &
1043 Fromonteil, 2021), and species richness (Janicke *et al.*, 2018). Yet, estimates of sexual
1044 selection present several constraints regarding how they are computed, which was the main
1045 subject of some meta-analyses (e.g. how mating success is measured and whether zero
1046 mating success is included; Anthes *et al.*, 2017; Macedo-Rego *et al.*, 2020a). Note that these
1047 estimates of sexual selection do not actually take into consideration effects of mate quality
1048 (see Fitzpatrick, 2015).

1049 At last, we found two meta-analytical studies with unique perspectives in the
 1050 literature. First, Cally *et al.* (2019) assessed fitness consequences on a population level from
 1051 experiments that enforced monogamy or manipulated adult sex ratio, essentially modulating
 1052 sexual selection. Second, Gómez-Llano *et al.* (2023) evaluated the costs imposed by one
 1053 sex's on the fitness of the other sex through direct (e.g. traumatic insemination) and/or
 1054 indirect (e.g. harassment) harm, the only study on sexual conflict in our dataset.

1055

1056 *(6) Further challenges and recommendations*

1057 Conducting a meta-analysis on a topic related to sexual selection can be an arduous process.
 1058 This is because this field presents many conceptual and analytical challenges that are rarely
 1059 addressed. In this section, we discuss these challenges and provide recommendations for
 1060 future work in the field of sexual selection, both for empiricists and researchers conducting
 1061 meta-analyses (summarised in Table 2, see also Nakagawa *et al.*, 2017).

1062

1063 Table 2. Recommendations for meta-analytical research projects on topics related to sexual
 1064 selection. Some of these recommendations can also be applied on projects with other
 1065 methodological approaches in this field (in grey). FAIR stands for Findable, Accessible,
 1066 Interoperable, Reusable (see Wilkinson *et al.*, 2016).

Item	Summarised recommendations	Manuscript section(s)
Research team	<ul style="list-style-type: none"> Form diverse and inclusive research teams (e.g. gender equal) Consider inviting researchers from the Global South for collaborations 	III.6.d
Research question and scope	<ul style="list-style-type: none"> Be mindful of the extent that certain taxa and topics related to sexual selection have received and your potential contribution to existing biases in the literature 	III.2.a, III.2.e, III.5

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

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

1067

1068 (a) Inclusion of humans

1069 Darwin's (1871) book "The descent of man, and selection in relation to sex" addresses
1070 human evolution and sexual selection (Ruse, 2015). At times, Darwin (1871) explicitly mixed
1071 these topics, using several examples from human society to support his arguments related to
1072 sexual selection. Using our own experiences to understand nature is intuitive (Kokko, 2017),
1073 and perhaps many scientists believe that studying other animals' reproductive behaviours can
1074 help us to comprehend ourselves. Indeed, we are only one among many species in the tree of
1075 life, and we often use our knowledge on other creatures to our direct benefit. However, we
1076 show a distinct aspect from other animals: an extremely complex culture that has a strong
1077 effect on our behaviours, including the ones related to reproduction (Eagly & Wood, 1999).
1078 For instance, culture influences which phenotypes are deemed attractive (Silverstein *et al.*,
1079 1986) and pair formation can be subjected to the decision of others (e.g. parents' influence;
1080 Buunk, Pollet & Dubbs, 2012). Additionally, people may choose to have few or no children
1081 through celibacy, contraception methods, or abortion, meaning that reproductive success
1082 plainly loses its utility in sexual selection studies when compared with other organisms.

1083 Issues from including humans in meta-analyses of sexual selection are not only
1084 problematic for behavioural traits: selection on humans has been modified or even nullified
1085 as we increasingly control our environment. For instance, crooked teeth in humans became
1086 common only recently, after we started eating processed (soft) foods that relaxed selection for
1087 large jaws that could accommodate all of our teeth (Corruccini, 1984; Lieberman *et al.*,
1088 2004). Thus, even for traits that are not under direct influence of culture (e.g. sperm traits),
1089 the distinct evolutionary pressures on modern humans might mislead comparisons with other

1090 organisms. This argument also applies for domesticated animals, as the process of artificial
1091 selection applied on them can modify their traits, as noted by Mautz *et al.* (2013).

1092 We ultimately recommend to evolutionary biologists to exclude humans from meta-
1093 analyses on topics related to sexual selection with other animals for the reasons above.
1094 Furthermore, the thought of humans as “just another species” is humble, but can also lead to
1095 anthropomorphisation of other organisms. This might be especially relevant for how we think
1096 of males and females (and their reproductive patterns; see section III.2.f), as our gender
1097 notions may affect our perceptions of them (Ahnesjö *et al.*, 2020; Pollo & Kasumovic, 2022).
1098 For example, Darwin (1871) argued that women are inferior to men, among other conclusions
1099 based on his observations from the Victorian society he lived in, which were described as
1100 processes emerging from our biology. A potential consequence of this type of rationale is
1101 falling into a vortex of self-affirmation, in which our societal views influence our notion of
1102 sex differences in nature and *vice versa*. In fact, part of the field of evolutionary psychology,
1103 a field born out of evolutionary biology from the 1970s (strongly based on Trivers, 1972; see
1104 also Fausto-Sterling *et al.*, 1997), seems to have succumbed to this pattern as they recurrently
1105 overemphasise gender differences (Eagly & Wood, 1999; Stewart-Williams & Thomas,
1106 2013). Studies from evolutionary psychologists commonly rely on assumptions related to
1107 other animals and ancestral human societies (for which information is scarce) to make
1108 hypotheses on current human behaviours (e.g. Geary, 2021). For instance, Lewis *et al.* (2017)
1109 claimed that high-heels make women more attractive because they can increase women’s
1110 lumbar curvature, representing a morphological adaptation for child bearing that would
1111 ultimately signal their high-quality to men. Lewis *et al.* (2017), however, barely mentioned
1112 alternative non-biological explanations to why women are deemed more attractive in high
1113 heels (e.g. influence of media). In addition, the authors completely ignored any historical
1114 relevant facts about high-heels, including that they were also used by men and were a symbol

1115 of masculinity for seven centuries before being associated with femininity in the 18th century
1116 (Semmelhack, 2020). This shows that reducing human behaviours to a simple biological
1117 product, which is an assumption implicitly made by meta-analyses related to sexual selection
1118 that include them with other species, can have profound consequences. If researchers strongly
1119 disagree with our stance of excluding humans from meta-analyses with other animals, we
1120 suggest that they at least include additional analyses, in which effect sizes obtained from
1121 humans are subsetting to assess their role in the study's conclusions (as in Fromonteil *et al.*,
1122 2023).

1123

1124 (b) Conceptual challenges and recommendations

1125 Darwin (1859, 1871) founded the field of sexual selection using jargon: he extensively used
1126 the terms “primary sexual characters” and “secondary sexual characters” in his work
1127 (attributing their creation to the surgeon and anatomist John Hunter). These terms, mainly
1128 secondary sexual characters, served as the backbone for Darwin's arguments on the existence
1129 of sexual selection. Whilst primary sexual characters refer to traits necessary for reproduction
1130 (e.g. gonads and genitalia), secondary sexual characters were used by Darwin to refer to traits
1131 that would supposedly be linked to mate acquisition but not reproduction itself. Secondary
1132 sexual characters are usually classified as ornaments (mate attraction) or weapons
1133 (intrasexual combat), which also became ubiquitous terms in the literature related to sexual
1134 selection (e.g. Andersson, 1994; Andersson & Iwasa, 1996; Andersson & Simmons, 2006;
1135 Shuker, 2010; Hosken & House, 2011; Simmons, Lüpold & Fitzpatrick, 2017; Lindsay *et al.*,
1136 2019). Such popularity can also be seen for the term “sexual signal” (whose exact origin is
1137 unknown to us, but probably from the 1980s; e.g. Endler & McLellan, 1988; Endler, 1992),
1138 which highlights the communicative function (i.e. role in inter-individual interactions) of
1139 secondary sexual traits.

1140 Researchers interested in related topics to sexual selection commonly employ this
1141 jargon when describing their question and selection criteria in meta-analyses. However, the
1142 expressions mentioned above are vague and loosely used, potentially causing transparency
1143 issues. For instance, numerous traits are frequently classified as secondary sexual
1144 characteristics simply based on sexual dimorphism, without a proper examination of its role
1145 on mate acquisition or reproductive success. This practice creates problematic cases, such as
1146 body size, which is explicitly mentioned as a secondary sexual trait by some (e.g. Simmons *et*
1147 *al.*, 2017). Although indeed there is evidence that males in many species benefit from larger
1148 bodies in male-male contests, leading to sexual selection on this trait and sometimes male-
1149 biased size dimorphism (Andersson, 1994), this pattern is simply assumed at times. An
1150 example can be seen in Moore & Wilson (2002), who relied exclusively on sexual size
1151 dimorphism as a proxy for sexual selection without evidence that body size was truly relevant
1152 to reproduction in all species investigated. The precarity of this assumption becomes evident
1153 when several cases of sexual size dimorphism occur due to other types of selection on body
1154 size, such as fecundity selection resulting in females larger than males in many invertebrates
1155 (but see Pincheira-Donoso & Hunt, 2017). Furthermore, if secondary sexual characteristics
1156 are synonymous with sexually selected traits (see Wiens & Tuschhoff, 2020), then this term
1157 could also encompass primary sexual traits, which are often under sexual selection (e.g.
1158 genitalia can play a role in post-copulatory competition; Andersson & Simmons, 2006).
1159 Similarly, traits related to gametes (e.g. sperm velocity) appear to be in a conceptual limbo,
1160 as they are rarely associated with this lingo despite also being determinant for post-
1161 copulatory processes (but see Rico-Guevara & Hurme, 2019).

1162 Mentioning sexual ornaments also requires clarification, as this expression simply
1163 alludes to shiny, elaborate, or extravagant traits used to attract mates. The fact that the word
1164 ornament has a colloquial meaning that predates its scientific (sexual) meaning is not a

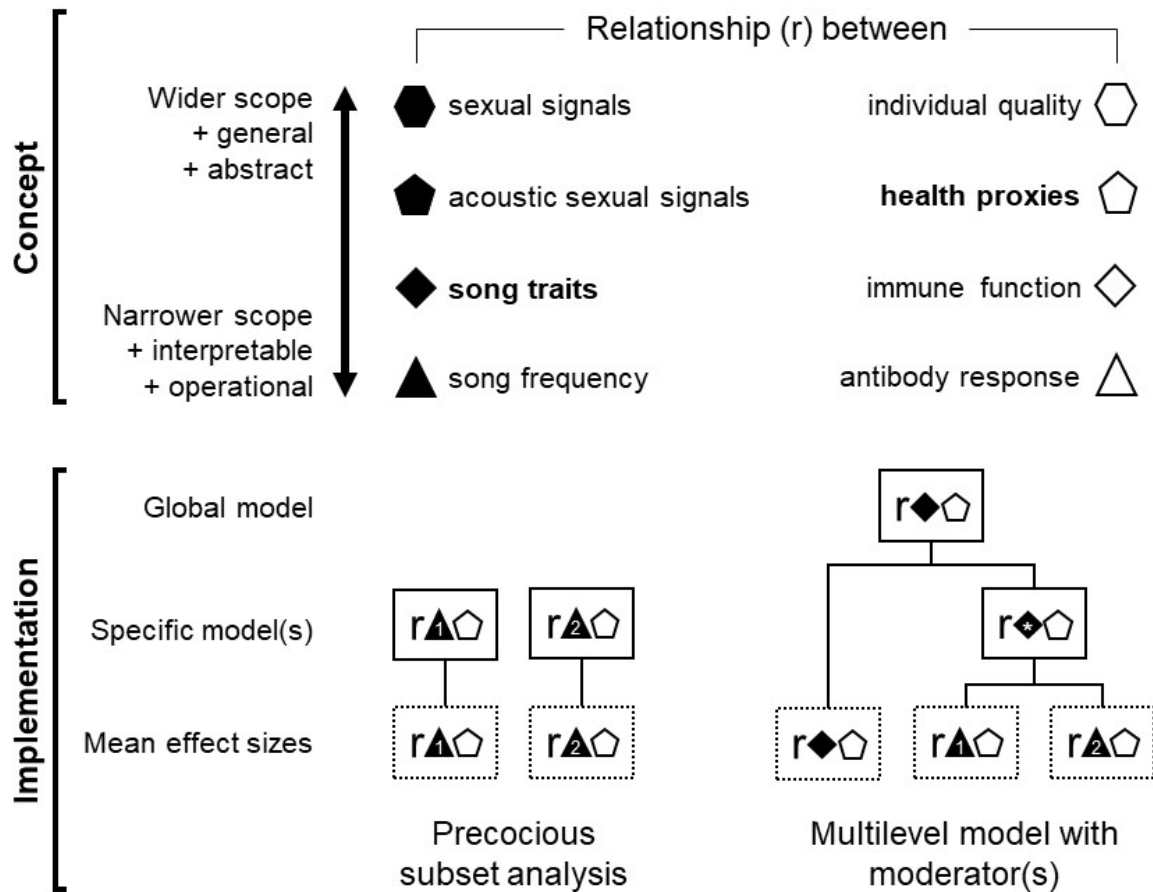
1165 coincidence: we tend to be fascinated by what catches our eyes or ears, revealing that our
1166 own sensory bias might not be reliable to describe all traits and patterns existing in nature.
1167 Thus, at least theoretically, other kinds of traits (e.g. chemical, tactile, electric; Kramer, 1990;
1168 Johansson & Jones, 2007) can also be classified as ornaments despite being inconspicuous to
1169 us. Although we cannot escape our human condition when observing nature (see Kokko,
1170 2017), it is crucial to acknowledge our biases, especially in meta-analyses that claim to
1171 explore general patterns related to sexual ornaments (section III.5.a). This also applies for
1172 other terms, such as weapons and sexual signalling, which tend to be used for morphological
1173 structures and acoustic displays, respectively. Moreover, sexual ornaments and sexual signals
1174 seem to be overlapping concepts, although the latter might also encompass signals used
1175 during agonistic encounters (e.g. threat signals). Overall, the many inconsistencies in the use
1176 of these expressions reveal that their careless application can be dangerous and misleading.

1177 Ultimately, the words researchers choose to describe their questions are pivotal
1178 because they define its scope and the required degree of detailing what exactly is being
1179 studied. The specific expressions linked to sexual selection we mentioned in this section tend
1180 to be quite abstract and thus represent a wider scope than specific terms that depict direct
1181 measurements (e.g. sexual signal vs. song frequency, respectively; Figure 16). The larger the
1182 scope of a question, the more likely the diversity of measurements included in a meta-
1183 analytical study will be (e.g. more distinct traits, methods, taxa), increasing the apparent
1184 generality of the results at the cost of its interpretability (Figure 16; Spake *et al.*, 2022). The
1185 fact that many meta-analyses have a wide scope possibly explains the common pattern of
1186 high heterogeneity found in meta-analytical studies in ecology and evolution (Senior *et al.*,
1187 2016a). Greater heterogeneity means that a global effect size has less reliability and that
1188 moderators are decisive in understanding patterns (Spake *et al.*, 2022). In other words, the
1189 motto invoked by biologists “it depends” intensifies with heterogeneity. However, studies

1190 with wide scope questions receive more attention and usually get published in prestigious
1191 journals precisely because they claim to settle theoretical conundrums with a single, concise
1192 estimate. Such a practice means that the studies that carry the most responsibility to untangle
1193 complex patterns are commonly the ones that highlight superficial results while downplaying
1194 their limitations. For instance, García-Roa *et al.* (2020) claimed to examine the effect of
1195 temperature on sexual selection, but details of their dataset could only be found in their
1196 supplementary material (very little information in-text). A closer inspection on their data
1197 reveals that most effect sizes for females were based on fecundity, which is far from being
1198 strictly related to sexual selection, casting doubt on the general validity of García-Roa *et al.*
1199 (2020)'s claims. Many other meta-analysis in our systematic map show a similar problem,
1200 asking wide scope questions with unclear sexual traits or sexual selection proxies (e.g. Møller
1201 & Alatalo, 1999; Møller, Christe & Lux, 1999; Weir *et al.*, 2011; Cally *et al.*, 2019; Hasik &
1202 Siepielski, 2022).

1203 As we showed, the specific expressions linked to sexual selection refer to diverse
1204 traits and patterns found in nature, being inherently loosely defined. Researchers thus need to
1205 be careful when using these terms in meta-analyses, clarifying what they truly encompass so
1206 readers can understand their study's focus and limitations. Clarification can be done by
1207 choosing the appropriate words that describe their research questions and goals (Figure 16) as
1208 well as by showing detailed information on the data searched and utilised in the manuscript
1209 (not just in the supplementary material). Finally, we emphasise that, as the scope of a
1210 question (and consequently of the study) gets wider, moderators and meta-regressions
1211 become increasingly necessary to avoid false generalisations (Nakagawa *et al.*, 2017; Spake
1212 *et al.*, 2022; see section III.6.c).

1213



1214

1215 Figure 16. Meta-analytical challenges in sexual selection using (Garamszegi, 2005) as an

1216 example. Top section shows how the scope of a question (e.g. whether two variables are

1217 related, denoted as “r”) is associated with the exact words used to describe it, in which shapes

1218 with more vertices represent wider scope. Terms in bold highlight our suggestion for a

1219 general question in (Garamszegi, 2005) (see text). Bottom section illustrates possible

1220 analytical implementations, with different options of meta-analytical models (solid line

1221 boxes) and their respective estimated mean effect sizes (dotted line boxes). A multilevel

1222 model with moderator(s) is recommended to estimate a global mean effect size that matches a

1223 general question (see text). Numbers inside shapes represent different subgroups (e.g. 1 =

1224 song frequency, 2 = song complexity), while a star (*) inside a shape represents the use of a

1225 moderator within a meta-analytical model.

1226

1227 (c) Analytical challenges and recommendations

1228 Several papers and books specifically targeted at ecology and evolutionary biologists provide
1229 helpful recommendations on how to conduct meta-analyses. Their focus ranges from initial
1230 procedures that are also part of systematic reviews (e.g. search and screening) to specific
1231 statistical methods (e.g. Nakagawa & Cuthill, 2007; Nakagawa & Santos, 2012; Koricheva *et*
1232 *al.*, 2013; Noble *et al.*, 2017; Foo *et al.*, 2021; O’Dea *et al.*, 2021; Nakagawa *et al.*, 2021;
1233 Spake *et al.*, 2022; Yang *et al.*, 2023b). Nonetheless, we noticed that many meta-analyses
1234 included in our systematic map conduct precocious subset analyses (i.e. practice of
1235 partitioning the extracted data and then fitting a separate meta-analytical model on each
1236 subset without a global model; Figure 16). This procedure often leads to a mismatch between
1237 the general question asked in the study and its respective statistical analysis. In this section,
1238 we use a fairly simple meta-analysis (Garamszegi, 2005) to illustrate our argument.

1239 Garamszegi (2005) examined the relationship between distinct bird song traits and
1240 health proxies (e.g. parasite prevalence or immune function). Intuitively, one can assume that
1241 this study asks “is song expression associated with health proxies?”. Yet, Garamszegi (2005)
1242 shattered the expectation of a single answer (e.g. through a global mean effect size) by
1243 presenting four separate mean effect sizes, each related to a different song trait (performance,
1244 complexity, duration, and frequency). This exemplifies precocious subset analysis, and we
1245 argue that this approach generates two issues.

1246 First, the reader is left without an answer to a general question (even if it is a vague
1247 one). Garamszegi (2005) only provides answers to separate, specific questions (e.g. does song
1248 frequency reflect health?; does song complexity reflect health?; etc). Second, subset analysis
1249 could increase error type I (i.e. rejecting a null hypothesis that is actually true) when
1250 compared with a unified, random-effects (multilevel) model (cf. Nakagawa & Santos, 2012;
1251 Nakagawa *et al.*, 2022). Third, effect sizes from groups analysed with different models

1252 cannot be statistically compared. Fourth, it limits the test of other moderators and their
1253 interactions. For example, Crean & Senior (2019) verified the effect of high-fat diets on
1254 model mammals regarding different sperm traits and several measurements of reproductive
1255 success, but each of these traits and measurements (17 in total) was analysed separately,
1256 meaning that the role of moderators (diet duration, specimen age, etc) could not be assessed
1257 across all effect sizes (only within each subset). Why analytical fragmentation has been
1258 employed so often is unclear, but we suspect that researchers' concern of being accused of
1259 making unfair comparisons through wider-scope models has increased the use of this
1260 approach. Alternatively, researchers may simply believe that each sub-question requires a
1261 separate meta-analytical model. Regardless of the reason, we believe it is crucial to discuss
1262 the benefits and disadvantages of each approach.

1263 Analysing data separately may seem fair at first glance: meta-analyses are often
1264 criticised for clumping conceptually distinct data to make inferences (i.e. “mixing apples and
1265 oranges”; Arnqvist & Wooster, 1995; Noble *et al.*, 2022). Although meta-analyses in other
1266 fields are not exempt from this complaint, the diversity of methodologies, biological traits,
1267 mechanisms, and patterns across species and empirical studies makes meta-analyses in the
1268 field of ecology and evolution particularly prone to this criticism. However, researchers have
1269 little option other than categorising measurements to make comparisons. For example,
1270 although Garamszegi (2005) analysed song traits separately, each one of them still included
1271 different measurements (e.g. song frequency involved both lowest and highest frequency, as
1272 well as frequency range). Moreover, parasite prevalence and immune function were analysed
1273 together, revealing that this author deemed them analogous measurements. Therefore,
1274 subsetting the analysis did not avail Garamszegi (2005) to entirely escape from mixing apples
1275 and oranges, essentially because it is inevitable to do so to a certain extent (Rosenthal, 1991).

1276 We suggest to researchers to, foremost, carefully define a question using the
1277 PECO/PICO framework (Richardson *et al.*, 1995; Foo *et al.*, 2021) that encapsulates all
1278 subquestions (if possible). Although multiple specific questions can be asked in a single
1279 meta-analytical study, they often can be summarised into a more general one, as we have
1280 shown for Garamszegi (2005) (Figure 16). This allows researchers to conduct one or few
1281 models with predictors (i.e. moderators) that can potentially explain the variation found,
1282 emphasising their effectiveness or lack thereof in doing so (Spake *et al.*, 2022), instead of
1283 fragmenting the data and analysis into multiple subsets from the start (Figure 16). These
1284 moderators fundamentally work as the specific questions that many authors ask when using
1285 subset analyses. A global model, however, becomes inadvisable when sub-questions are
1286 completely unrelated to one another so a more general question becomes infeasible (although
1287 this might be subjective) or when effect sizes calculated are distinct in nature (based on
1288 means vs. based on variances). This approach makes it even more critical that authors specify
1289 the direction of calculated effect sizes for each measurement before analysis, preferably
1290 based on grounded hypotheses (e.g. Dougherty, 2021a). Nonetheless, the direction of effect
1291 sizes can be modified ad-hoc if one of the subsets presents an opposite pattern, so that the
1292 global mean effect size can focus on magnitude rather than direction.

1293 Researchers might still harbour suspicion over a global model approach in complex
1294 cases as, until now, we have only used a meta-analysis with relatively specific questions as an
1295 example (Garamszegi, 2005). Thus, consider Alissa (2018), who asked whether limitation in
1296 reproductive sites is associated with several measurements related to sexual selection (e.g.
1297 pre-copulatory intrasexual competition, sperm competition, selection on male traits, and
1298 opportunity for sexual selection). In this study, the author conducted several meta-analyses
1299 (i.e. subsets were independently analysed), probably because of wildly distinct measurements
1300 included in it. Although it would not be possible to combine opportunity for sexual selection

1301 with the other measurements because they are represented by distinct types of effect sizes in
1302 the study (lnCVR and Zr, respectively), all else could be grouped together. Grouping the
1303 effect sizes to estimate a single mean effect size would allow the author to compare the effect
1304 sizes for each measurement related to sexual selection. In truth, this global effect size would
1305 represent a more abstract and less interpretable estimate: whether reproductive site limitation
1306 is associated with various measurements related to sexual selection (see section III.6.b).
1307 However, the existence of a global mean effect size does not preclude researchers to focus on
1308 specific, narrow questions, which can be done with moderators and meta-regressions. Doing
1309 so would maintain the original conceptual structure in Alissa's (2018) manuscript while
1310 correcting its analysis.

1311 Our recommendation to unify multiple, usually related questions to fit a single (or as
1312 few as possible) meta-analytical model does not mean to incentivize wider questions, but
1313 rather attempts to streamline analyses. In fact, focused meta-analyses (i.e. with narrow
1314 questions) can be more reliable because they are easy to interpret (Figure 16). Conversely, as
1315 previously mentioned (see section III.6.b), studies with wide questions that employ few or no
1316 meta-regressions might be of little use if they show highly heterogeneous estimates. Although
1317 the use of moderators might be constrained (e.g. due to too few data points), authors should at
1318 least justify these limitations and consider them to avoid misleading conclusions.

1319

1320 (d) Authorship diversity

1321 Our bibliometric analysis suggests that authors conducting meta-analyses on topics associated
1322 with sexual selection are often men based in developed countries (see section III.4), which is
1323 a pattern often found in academia (Astegiano, Sebastián-González & Castanho, 2019; Huang
1324 *et al.*, 2020). We note, however, that our analysis regarding countries is purely based on
1325 affiliations listed, meaning that authors could be of a different nationality (i.e. immigrants).

1326 For instance, although four of the authors of the present study are affiliated to the same
1327 Australian university, none was born in Australia. Still, the existence of international and
1328 intercontinental collaborations we found reiterate the globalisation of science (Gui, Liu & Du,
1329 2019), although concentrated in the Global North (i.e. developed countries).

1330 While patterns of research production for countries may follow economic trends (e.g.
1331 amount of public funding to research in each country; Gush *et al.*, 2018), gender inequity in
1332 research production has multiple explanations. First, it might be a consequence of a “leaky
1333 pipeline” that precludes women from filling higher academic positions as often as men (Shaw
1334 & Stanton, 2012; McDermott *et al.*, 2018). This is also seen in boards of scientific societies,
1335 in which women are outnumbered by men (Potvin *et al.*, 2018). Intuitively, this entails fewer
1336 opportunities for women to conduct research. In addition, there is a gender gap in
1337 productivity in which women are outperformed by men, even in gender equal academic
1338 faculties (Astegiano *et al.*, 2019). This can be a consequence of differential pressures on
1339 women, compared with men, from inside (e.g. lower salary and more time spent in
1340 administrative tasks; DesRoches *et al.*, 2010) and outside (e.g. family caring; Fox, Fonseca &
1341 Bao, 2011) of academia.

1342 The patterns we found regarding countries and gender are not limited to this specific
1343 literature, but simply another example of a more generalised problem in academia and
1344 research production overall. Yet, this does not mean we should accept this pattern idly.
1345 Rather, it emphasises that actions are needed to change this precarious situation as diversity
1346 can promote creativity (McLeod, Lobel & Cox, 1996) and innovation (Nieto & Santamaría,
1347 2007), ultimately being beneficial to science (Intemann, 2009; Cheruvilil *et al.*, 2014). The
1348 most obvious example of benefits brought by diversity in the context of meta-analyses comes
1349 from the inclusion of people with distinct language skills (e.g. from different countries) that
1350 can increase the coverage of the literature retrieved beyond just papers in English (Amano *et*

1351 *al.*, 2023). Furthermore, people of distinct nationalities can also vary in how they perceive
1352 stereotypes related to sexual behaviours in nature, making diverse teams more open to
1353 various perspectives (Pollo & Kasumovic, 2022).

1354 Several solutions have been proposed to ameliorate these diversity issues. For
1355 instance, researchers from the Global North should actively and fairly collaborate with
1356 researchers from the Global South (see more suggestions in Haelewaters, Hofmann &
1357 Romero-Olivares, 2021 and in Nakamura *et al.*, 2023). Furthermore, many actions are being
1358 employed by different institutions to address gender disparity observed in academia, but they
1359 are rarely applied on a large scale or are ineffective (see Casad *et al.*, 2021) and references
1360 within). Yet, gender and country of affiliation or origin are just a few of several aspects that
1361 matter to diversity. For instance, people of colour (Evangelista *et al.*, 2020) and from lower
1362 economic backgrounds (Lee, 2016) are commonly excluded from academia, revealing a need
1363 to develop ways to include these marginalised groups as well.

1364

1365 (e) Beyond meta-analyses

1366 Throughout our manuscript, we identified several biases related to the content of meta-
1367 analyses on topics related to sexual selection (e.g. on specific questions, taxonomic groups,
1368 focal sex, etc). However, this might simply be a reflection of biases that already occur in the
1369 primary literature on sexual selection. For instance, although researchers might be interested
1370 in meta-analytical questions that can encompass all animals, data available are highly
1371 concentrated in certain animal groups (e.g. birds; see section III.2.a). Thus, it might be
1372 fruitless to expect that researchers interested in meta-analyses can solve these biases alone if
1373 the raw material (primary evidence) remains unchanged. In fact, proper meta-analyses are
1374 also systematic reviews, highlighting gaps in the primary literature and therefore serving as
1375 indicators of the extent of our empirical knowledge.

1376 One source of generalised biases in the literature may lie in the current publishing
1377 system, which shows an obsession with “novelty” (Cohen, 2017; Brembs, 2019; Ottaviani *et*
1378 *al.*, 2023). Paradoxically, novelty is rarely defined by journals that request it, but possibly
1379 refers to new and impactful discoveries, albeit this is highly subjective (Brembs, 2019). On
1380 one hand, this can encourage the production of meta-analyses because of their great power to
1381 test hypotheses (but see section III.6.c). Indeed, meta-analytical studies are often published in
1382 prestigious journals (e.g. Weaver *et al.*, 2018; Nolzco *et al.*, 2022). However, as previously
1383 mentioned, meta-analyses in ecology and evolution commonly detect high heterogeneity
1384 among effect sizes and often fail to find factors that can explain it, mainly because data are
1385 scarce. This means that continuing to generate empirical data is almost always necessary,
1386 regardless of the subject. Yet, the pursuit of novelty only reduces the reward of further
1387 empirical research on a topic, especially with methods, organisms (even if not the same
1388 species or even genus), or results that resemble already published papers. For example, a
1389 study on mate choice with a spider species becomes less valuable to the publishing system
1390 the more studies on mate choice there are with other spiders (even though there are more than
1391 50,000 species of spiders). This perspective makes empirical research harder to publish in
1392 top-tier journals, ultimately discouraging scientists from producing empirical data that would
1393 be extremely valuable to build a solid foundation of the theory. In a system that hampers
1394 research endeavours because of some similarity with previous work, replication becomes
1395 almost impossible despite being pivotal to science (Kelly, 2006; Nakagawa & Parker, 2015;
1396 Fraser *et al.*, 2020).

1397 Limited research replication has many negative impacts on meta-analyses. Not only
1398 does it reduce the amount and strength of empirical data available, but also precludes updates
1399 of meta-analyses as this can be seen as “not novel”. Our study actually shows that many
1400 meta-analyses on topics related to sexual selection should be redone, both because new data

1401 has accumulated since they were published and because of their substandard methods and
1402 reporting (see section III.3). Moreover, the fact that numerous decisions in a research project
1403 can generate different outputs (Gelman & Loken, 2013) also applies to meta-analyses. For
1404 instance, some meta-analytical studies addressed almost identical questions but had their own
1405 particularities and sometimes reached distinct conclusions (e.g. Pollo *et al.*, 2022; Dougherty,
1406 2023). This only emphasises that how research is conducted is as important, if not more, than
1407 how novel the question or methods are. Therefore, we deem innovation as pivotal to
1408 advancements in the field of sexual selection as long as it does not sacrifice further research
1409 of superficially explored topics.

1410

1411 **IV. Conclusions**

1412 (1) The vastness of the field of sexual selection can be seen in more than 150 meta-analyses
1413 on topics associated with it. Although the first of these studies was published more than 25
1414 years ago, most of them were conducted in the last decade.

1415 (2) We found numerous biases in these meta-analytical studies. Most of them concentrated on
1416 birds or insects (taxonomic bias) and on male traits or patterns (conforming sex bias).
1417 Furthermore, although the questions asked in these studies were diverse, many concentrated
1418 on pre-copulatory sexual traits, such as weapons and ornaments. Thus, we call for greater
1419 research attention to females, underexplored animals, and neglected topics such as post-
1420 copulatory processes.

1421 (3) The reporting quality of meta-analyses in the field of sexual selection is often poor,
1422 indicating that many might be unreliable. This problem is particularly strong for sharing of
1423 raw data and analysis scripts, revealing a dire need to improve these issues in future meta-
1424 analyses.

1425 (4) We observed both geographical and gender bias in respect to researchers that conducted
1426 meta-analyses on topics related to sexual selection. Specifically, most of these papers were
1427 authored by men based in developed countries, signalling that gender and socio-cultural
1428 diversity might be lacking in the field of sexual selection. This reiterates the need for
1429 including minority groups in academia.

1430 (5) We noticed that meta-analyses on topics related to sexual selection commonly employ
1431 detrimental conceptual and methodological approaches. We therefore recommend to authors
1432 to avoid including humans with other species in meta-analytical studies in this field, to be
1433 careful with loose terms that are part of the sexual selection jargon, and to use global meta-
1434 analytical models with moderators to make inferences. This, however, should be a
1435 consequence of a well thought plan that starts at the inception of the study, with a well
1436 formulated question and specific hypothesis.

1437 (6) Despite our focus on meta-analyses, many of the issues pointed out here can be an
1438 extension of problems occurring in the primary literature (content) and in academia (authors).
1439 Thus, our manuscript possibly serves as a status report for the whole field of sexual selection.

1440

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1445

1446 **VI. Author contributions**

1447 Conceptualisation: P.P., M.L., S.N.; data curation: P.P.; formal analysis: P.P.; funding
1448 acquisition: S.N.; investigation: P.P., M.L., Y.Y., A.C., S.N.; methodology: P.P., M.L., S.N.;

1449 project administration: P.P., S.N.; software: P.P.; supervision: S.N.; visualisation: P.P.;
1450 writing - original draft: P.P., S.N.; writing - review & editing: P.P., M.L., Y.Y., A.C., S.N.

1451

1452 **VII. Data availability**

1453 The supplementary material is available at https://pietropollo.github.io/map_sexual_selection.

1454

1455 **VIII. References**

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