1   **Synthesis of nature's extravaganza: an augmented meta-meta-analysis on (putative)**

2   **sexual signals**

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12 **Abstract**

13 Conspicuous characteristics that do not seem to contribute to the survival of their bearers,

14 such as colourful body parts and bizarre behaviours, have puzzled biologists for centuries.

15 Sexual selection theory posits that these characteristics evolved because more conspicuous

16 individuals attract more mates and experience greater fitness, yet evidence for this remains

17 fragmented. Our augmented meta-meta-analysis of 41 meta-analyses, encompassing 375

18 animal species and 7,428 individual effect sizes, shows that the conspicuousness of (putative)

19 sexual signals is positively related to attractiveness and benefits to mates, as well as to the

20 fitness, condition, and other traits (e.g. body size) of signal bearers. Importantly, most of

21 these patterns are consistent across both taxa and sexes once within-study variation is

22 considered, underscoring the generalisability of our results. However, we found evidence of

23 publication bias for some of these relationships, meaning some of our results need to be taken

24 with caution. Furthermore, the strength of sexual selection on conspicuousness is positively

25 associated with the relationship between (i) conspicuousness and fitness benefits and (ii)

26 conspicuousness and individual condition. Our study unifies several decades of knowledge on

27 conspicuous traits, provides new insights about them, and lays a clear path for the future of

28 this topic.

Main text

Extravagant body parts and elaborate behaviours that apparently are not used to deter predators (e.g. aposematic traits) or to fight (e.g. weapons) have intrigued biologists for more than a century precisely because natural selection can rarely explain their evolution[1]. These odd traits should be particularly conspicuous to conspecifics (hereby *conspicuous traits*), even though some of them might be unnoticeable to us (e.g. pheromones, electromagnetic fields). The usual explanation for the existence of these conspicuous traits is that more noticeable individuals can attract more or better mates, generating sexual selection for greater trait conspicuousness via mate choice[1–3]. Consequently, conspicuous traits are often deemed "sexual ornaments" or "sexual signals", especially if they are sexually dimorphic[4]. Unsurprisingly, mate choice and sexual signals became popular topics within the sexual selection literature since the 1970s, culminating in the development of many theoretical models attempting to explain their evolution (reviewed in ref. [5]). Despite varying their expectations, these models usually predict that sexual signal conspicuousness increases the fitness of their bearers (e.g. by making them more attractive) and of their mates by signalling direct (in the same generation, with resources or good parenting) or indirect benefits (in subsequent generations, enhancing offspring fitness with greater viability - "good genes" - or attractiveness - "sexy genes")[2,5,6]. The theory also predicts that sexual signal conspicuousness is condition-dependent[6] and that sexual signal conspicuousness covaries with the expression of other traits that can also represent benefits to prospective mates (e.g. body size, social dominance, traits related to sperm competition).

The veracity of the propositions above has been tested in the last several decades by numerous empirical studies and, more recently, by various meta-analyses (reviewed in ref. [4]). However, our knowledge of conspicuous traits assumed to be sexual signals remains fragmented and far from satisfactory because studies (including meta-analytical ones) focus

54 on one or few variables (e.g. parasite load[7]; survival[8]), types of conspicuous traits (e.g.

55 colourful plumage[9,10]; song traits[11,12]), taxa (e.g. birds[8–18]), and sex (e.g. males[19–21]). The last

56 one is particularly emblematic because most of the theory regarding sexual signals has been

57 developed considering only males as their bearers, even though females possess conspicuous

58 traits in many species[22] and males can express mate choice[23]. Moreover, researchers often

59 assume that conspicuous traits they investigate are attractive to prospective mates without

60 evidence, potentially mixing sexual signals with other non-sexually selected traits and thus

61 possibly drawing misleading conclusions on the evolution of conspicuous traits.

62   To resolve these outstanding issues, provide a unified knowledge of (putative) sexual

63 signals, and test the generality of patterns related to these signals, we compiled and analysed

64 7,428 effect sizes from 1,196 empirical studies (used as data sources by 41 meta-analyses[7–

65 21,24–49]; i.e. second-order meta-analysis augmented with additional data) that investigate the

66 relationship between these conspicuousness of these traits and their bearers' attractiveness,

67 fitness, individual condition, and other traits (Table S1; Fig. 1), representing 375 animal

68 species in total (Fig. 2). We note that determining the conspicuousness of a trait is particularly

69 challenging due to the numerous ways it can be evaluated, such as by their colouration

70 (which depends on many variables, e.g. brightness, chroma, hue), size, symmetry, duration,

71 or other specific properties (e.g. sound frequency). Nonetheless, we used a tailored approach

72 for each trait and species in our dataset using information provided by our data sources (i.e.

73 empirical studies and meta-analyses; see Table S2). We also verified the role of two

74 moderators in the relationships assessed in our study. First, considering that sexual selection

75 is typically proposed to act more strongly on males than on females[1,50,51], we assessed the

76 effect of the sex of signal bearers (male *vs.* female) on our results. Second, in comparison

77 with colour and morphology (hereby *fixed traits*), behavioural signals (hereby *flexible traits*,

78 available only for males in our dataset) can profusely vary in short periods and thus are more

79   likely to reflect their bearers' current condition[24], so we also tested the role of trait type

80   (flexible *vs.* fixed) when conducting our analyses. Furthermore, we verified an implicit

81   assumption commonly made by biologists that, to our knowledge, has never been

82   systematically tested across studies or species: that the strength of pre-copulatory sexual

83   selection (from mate choice) on the conspicuousness of a trait is linked to the strength of the

84   relationship between the conspicuousness of that trait and the benefits it signals[52,53], and by

85   extension to the relationship between the conspicuousness of that trait and the fitness,

86   condition, and other traits of its bearer.

87

88   **Results and discussion**

89   *Is the conspicuousness of putative sexual signals associated with attractiveness to prospective*

90   *mates?*

91   Empiricists commonly take different measurements from one or more conspicuous traits of

92   individuals of a given species (e.g. refs. [54–56]). They then verify the relationship between these

93   measurements and success in mate choice trials or number of mating (i.e. mating success) in

94   the field, which should roughly represent the strength of pre-copulatory sexual selection on

95   conspicuous traits. Using this type of data, we found that putative sexual signal

96   conspicuousness is, on average, (moderately) positively related to attractiveness to

97   individuals of the opposite sex ($r = 0.329$, 95%CI $= 0.233$ to 0.419; Table S3; Fig. 3). This

98   result is consistent across species given the low heterogeneity at the level of species ($I^2_{[\text{species} = }$

99     $_{\text{species ID + phylogeny}]} = 2.3\%$) and therefore potentially generalisable, despite the high overall

100   heterogeneity across effect sizes ($I^2_{\text{total}} = 91.5\%$; Table S4).

101

102   *Is the conspicuousness of putative sexual signals associated with benefits to their bearers and*

103   *to their mates?*

104   Although our data primarily represent the benefits of putative sexual signal conspicuousness to the

105   bearers of such signals, these benefits are often shared with or originating from bearers' mates. For

106   example, the mating date or the number of eggs laid are influenced by traits and decisions of both

107   pairing individuals. Thus, we can only distinguish benefits to signal bears from benefits to their mates

108   in some occasions. We faced a similar issue when attempting to differentiate direct from indirect

109   benefits, as this requires a more complex approach than the one we provide here (see meta-analyses

110   exploring this in-depth, e.g. refs. [40,57]).

111   We found that putative sexual signal conspicuousness is, on average, (weakly) positively

112   related to benefits to their bearers and to their mates (r = 0.165, 95%CI = 0.133 to 0.197; Table S3;

113   Fig. 3). However, we detected evidence of publication bias for these data, so the actual relationship

114   might be even weaker as positive effect sizes were overrepresented (Fig. S1D-F, Table S7). This

115   finding is potentially consistent across species ($I^2_{[species = species ID + phylogeny]}$ = 0.7%; Table S4).

116   Furthermore, we found that males show, on average, a stronger relationship between putative sexual

117   signal conspicuousness and benefits compared with females (Table S5). We note that these results

118   come from an amalgamation of metrics (Fig. 1), so we discuss each of them in detail below.

119   First, more conspicuous putative sexual signals are, on average, (moderately)

120   associated with earlier arrival at breeding sites, earlier pairing, or earlier reproduction (hereby

121   simply *earlier timing*; r = 0.213, 95%CI = 0.171 to 0.254; Table S3; Fig. 3). Earlier timing

122   can represent individual quality and attractiveness, and may lead to more reproductive

123   opportunities and a better environment for the offspring[58]. We also found that the relationship

124   between timing and putative sexual signal conspicuousness is stronger in males than in

125   females (Table S5).

126   Second, putative sexual signal conspicuousness is, on average, (weakly) positively

127   related to reproductive success (e.g. number of offspring; r = 0.157, 95%CI = 0.121 to 0.193;

128   Table S3; Fig. 3). Various mechanisms can produce a positive relationship between

129   reproductive success and putative sexual signal conspicuousness. For instance, given that

130   individuals with traits that are more conspicuous tend to be more attractive, these individuals

131   should experience greater mating success and consequently increase their reproductive

132   success if mating with multiple individuals is advantageous (i.e. when Bateman's gradient is

133   positive, generally assumed for males but rarely for females[50]). Moreover, individuals with

134   more conspicuous sexual signals might be more likely to select mates that can provide them

135   with more benefits[23], increasing their own fitness. Individuals with more conspicuous sexual

136   signals may also receive greater reproductive investment from their partners than their

137   counterparts[59]. On the other hand, a positive relationship between sexual signal

138   conspicuousness and reproductive success can arise from a positive association between

139   putative sexual signal conspicuousness and (female) fecundity (e.g. refs. [60,61]) or reproductive

140   investment beyond just gametes (e.g. parental care, see below), which would make these

141   conspicuous traits signals of direct benefits to mates. Although we cannot determine which of

142   these mechanisms more frequently explains why individuals with more conspicuous putative

143   sexual signals show greater reproductive success, future studies should address this gap. We

144   also note that the conspicuousness of male flexible putative sexual signals is more strongly

145   associated with reproductive success than that of male and female fixed putative sexual

146   signals (Table S5).

147   Third, putative sexual signal conspicuousness is, on average, (weakly) positively

148   related to offspring viability (e.g. proportion of eggs hatched) or quality (e.g. offspring size,

149   see also Table S1) ($r = 0.164$, $95\%CI = 0.123$ to 0.205; Table S3; Fig. 3). More conspicuous

150   sexual signals may indicate that their bearers possess "good genes" that can be passed to the

151   offspring, possibly increasing offspring's viability and quality[2]. However, the same arguments

152   made for reproductive success (e.g. greater reproductive effort from partners) also apply to

153   offspring's viability or quality because they result from genes and investment in the offspring

154   from both parents.

Fourth, putative sexual signal conspicuousness is, on average, (weakly) positively related to greater extra-pair paternity and lower cuckoldry (collectively simply *paternity*; r = 0.149, 95%CI = 0.092 to 0.204; Table S3; Fig. 3). While this relationship might occur because more ornamented males are more attractive (i.e. paternity may simply reflect male mating success or be a product of cryptic female choice favouring sperm from attractive males), it is also possible that more ornamented males obtain greater paternity when their conspicuous putative sexual signals signal sperm traits that increase success in sperm competition[62].

Fifth, putative sexual signal conspicuousness is, on average, (weakly) positively related to the amount of parental care expressed by the signal bearer (r = 0.08, 95%CI = 0.022 to 0.136; Table S3; Fig. 3). This is perhaps the clearest evidence that conspicuous traits can signal direct benefits to mates. Still, this relationship might be complex in systems with biparental care if sexual signals from both parents affect parental care performed. This scenario becomes even more complicated when parental care provided by an individual can be modulated by the parental care provided by their social partner[10].

Sixth, putative sexual signal conspicuousness is, on average, (moderately) positively related to territory quality (r = 0.241, 95%CI = 0.162 to 0.317; Table S3; Fig. 3). Given that territory quality represents resources that individuals use for their survival and reproduction, greater territory quality should enhance the fitness of the territory's owner as well as of their mates. Unfortunately, our dataset had no information for females regarding this relationship, revealing a dire need to investigate species in which females defend territories (e.g. ref. [63]).

Is the conspicuousness of putative sexual signals associated with the individual condition of their bearers?

179 We found that putative sexual signal conspicuousness is, on average, (weakly) positively

180 related to distinct measures of individual condition (r = 0.174, 95%CI = 0.124 to 0.224; Table

181 S3; Fig. 4). Yet, this result can be overestimated as we found evidence of publication bias for

182 these data (Fig. S1G-I; Table S7). Once more, this result is potentially generalisable across

183 taxa ($I^2_{[species = species ID + phylogeny]}$ = 6.1%; Table S4). Moreover, we found that males show, on

184 average, a stronger relationship between fixed putative sexual signal conspicuousness and

185 individual condition compared with females (Table S5).

186   Individual condition can be measured in many ways (Fig. 1), so we also verified the

187 relationship between each individual condition proxy and putative sexual signal

188 conspicuousness separately. First, putative sexual signal conspicuousness is, on average,

189 (moderately) positively associated with beneficial (external) conditions (e.g. better diet, lower

190 reproductive effort, etc.; r = 0.263, 95%CI = 0.215 to 0.31; Table S3; Fig. 4). Second,

191 putative sexual signal conspicuousness is, on average, (weakly) positively associated with

192 body condition (e.g. body mass controlled for structural body size[64]; r = 0.198, 95%CI =

193 0.161 to 0.235; Table S3; Fig. 4). Yet, conspicuousness of fixed putative sexual signals is, on

194 average, more strongly associated with body condition in males than in females (Table S5).

195 Third, putative sexual signal conspicuousness is, on average, (weakly) positively associated

196 with immune or antioxidant capacity (r = 0.129, 95%CI = 0.084 to 0.174; Table S3; Fig. 4).

197 Fourth, putative sexual signal conspicuousness is, on average, (weakly) positively associated

198 with parasite resistance (i.e. opposite of parasite load; r = 0.119, 95%CI = 0.078 to 0.159;

199 Table S3; Fig. 4). Fifth, putative sexual signal conspicuousness is, on average, (weakly)

200 positively associated with survival (r = 0.113, 95%CI = 0.053 to 0.172; Table S3; Fig. 4).

201 However, the relationship between putative sexual signal conspicuousness and survival was

202 greater for males than for females, with the latter being essentially zero (Table S3; Table S5;

203 Fig. 4).

204   Two hypotheses in the literature explain how condition-dependent sexual signals

205   represent honesty: the costly signalling principle (first proposed by ref. [65]) and the index

206   hypothesis (e.g. ref. [66]). The former states that the expression and maintenance of sexual

207   signals require resources that could be spent elsewhere[65], with higher-quality individuals

208   being expected to deal more effectively with metabolic trade-offs and thus being able to be

209   more ornamented[67,68]. On the other hand, the index hypothesis does not invoke resource

210   trade-offs to explain sexual signals' condition-dependence, but rather posits that these traits

211   evolve as honest signals of condition by sharing pathways with basic physiological

212   processes[69–71]. These hypotheses are contentious as each has different underlying concepts,

213   with multiple authors proposing distinct features and predictions (see ref. [72]). Our results

214   support that (putative) sexual signal conspicuousness is, on average, condition-dependent, but

215   we cannot elucidate which of these two hypotheses is more likely to explain this pattern.

216

217   *Is the conspicuousness of putative sexual signals associated with the expression of other*

218   *traits of their bearers?*

219   We found that putative sexual signal conspicuousness is, on average, (moderately) positively

220   related to body size ($r = 0.23$, 95%CI = 0.144 to 0.312; Table S3; Fig. 4), an apparently

221   generalisable finding across species ($I^2_{[species = species\ ID + phylogeny]} = 3.6\%$; Table S4). Body size

222   can be under positive directional selection if larger individuals are more fecund[73] or

223   experience greater success in intrasexual competition[2]. Given that sexual signal

224   conspicuousness is also predicted to be under positive directional sexual selection[74], a

225   positive relationship between sexual signal conspicuousness and body size can occur. In such

226   a scenario, trait conspicuousness would signal direct benefits to prospective mates. However,

227   larger body size can be constrained or even disfavoured in some taxa (e.g. ref. [75]), so this

228   rationale is not universal.

229   We found that putative sexual signal conspicuousness is, on average, (moderately)

230   positively related to aggression and social dominance (e.g. greater number of aggressive

231   behaviours performed to hetero- and conspecific intruders; r = 0.205, 95%CI = 0.047 to

232   0.354; Table S3; Fig. 4). However, this result is not as generalisable across species as our

233   other findings ($I^2_{[species\ =\ species\ ID\ +\ phylogeny]}$ = 14.6%; Table S4). Greater trait conspicuousness

234   then may signal one's status to others interested in battling for resources, ultimately deterring

235   costly fights[76]. Note that, *a priori*, if these resources are not mates, these signals have no

236   connection to sexual selection, highlighting that conspicuous traits might not necessarily be

237   sexual signals. Yet, conspicuous traits that signal to rivals can also be used for mate selection,

238   even if this is not their primary function. After all, greater success in competition for

239   resources should be related to greater access to resources, meaning possible benefits to mates

240   (e.g. territory quality, more competitive offspring if heritable).

241   We found that putative sexual signal conspicuousness is, on average, (weakly)

242   positively related to the expression of traits that increase success in sperm competition (e.g.

243   more or better sperm, larger testes; r = 0.107, 95%CI = 0.029 to 0.185; Table S3; Fig. 4). This

244   result appears to be generalisable across taxa, but not across studies ($I^2_{[species\ =\ species\ ID\ +}$

245    $_{phylogeny]}$ = 1.2%, $I^2_{across-studies}$ = 43%; Table S4). Highly ornamented males could be wasting

246   resources by investing in traits related to sperm competition if, being more attractive, they

247   can experience a lower risk of sperm competition by biassing cryptic female choice in their

248   favour (e.g. ref. [77]) or reducing the chances that females they mate with remate with another

249   male (e.g. ref. [78]). However, traits that enhance sperm competition success are potentially

250   under positive directional selection for all males[31] (but see ref. [79]) and thus may be expected

251   to covary with sexual signal conspicuousness. Alternatively, this pattern can occur if male

252   ornamentation honestly signals their fertilisation ability to females[31]. Interestingly, we also

253 detected that flexible putative sexual signals were more strongly related to the expression of

254 sperm competition-related traits than fixed putative sexual signals (Table S5).

255 Lastly, we found that putative sexual signal conspicuousness is, on average, (weakly)

256 positively related to age (r = 0.196, 95%CI = 0.043 to 0.34; Table S3; Fig. 4), a result that

257 may be generalisable across species ($I^2_{[species = species\ ID + phylogeny]}$ = 7.4%; Table S4). Sexual

258 signal conspicuousness should increase with age (but see ref. [24]) as older individuals are

259 under greater terminal investment selection (i.e. to increase reproductive effort before

260 dying[80,81]). Moreover, when sexual signal conspicuousness is positively related to age, trait

261 conspicuousness essentially signals individual ability to survive for longer[82]. We note,

262 however, that our results regarding age might be conflated by mating experience (i.e. older

263 individuals are more likely to have mated than their younger counterparts), although a meta-

264 analysis controlling for this showed a similar result[24].

265

266 *Do sex and trait type play a role in the relationships assessed?*

267 As shown in previous sections, we found that, compared with male fixed putative sexual

268 signals, the conspicuousness of female fixed putative sexual signals is, on average, less

269 condition-dependent and more weakly related to the benefits provided to bearers and to

270 mates. However, these sex differences only emerged when analysing all proxies of these

271 variables together, or when evaluating some specific proxies separately, such as timing, body

272 condition, and survival. Therefore, our results only partially support the predictions that

273 originate from the idea that males are under stronger sexual selection than females[1,50,51]. Most

274 importantly, our findings indicate that the conspicuousness of putative sexual signals in both

275 males and females are, on average, associated with greater benefits to bearers and to mates,

276 greater individual condition, and body size. This emphasises that researchers need to consider

277 the role of individuals of both sexes when exploring processes and patterns related to sexual

278 selection.

279   In contrast with the effects of sex on our results, we found only a few instances in

280 which trait type played a role in the relationships between various factors and the

281 conspicuousness of putative sexual signals. More specifically, considering only male putative

282 sexual signals, the conspicuousness of flexible traits was more strongly related to signal

283 bearers' reproductive success and ability in sperm competition than fixed traits. These

284 findings might be affected by limited or absent data on behavioural signals in our dataset for

285 males and females, respectively. Still, we show that, indeed, different trait types are

286 associated with different patterns that are predicted by the theory of sexual selection, which

287 requires further attention from researchers.

288

289 *Is the strength of sexual selection on the conspicuousness of a trait associated with the*

290 *relationship between the conspicuousness of the same trait and other variables?*

291 The relationships between conspicuous traits and multiple variables we explored in previous

292 sections involved traits *assumed* to be preferred by mates (i.e. putative sexual signals). Still,

293 these traits could actually be unattractive to mates or attractive in the opposite direction than

294 the one predicted (e.g. preference for dull colours instead of vivid colours). To provide

295 insights into sexual signals, we sought putative sexual signals in our dataset for which we had

296 two pieces of information: how their conspicuousness was related to attractiveness to mates

297 and how their conspicuousness was related to other variables within our framework (e.g.

298 benefits, individual condition, etc.; Fig. 1). For each putative sexual signal of each species,

299 we calculated an overall effect size for the former (hereby *Zr-attractiveness*) and an overall

300 effect size for the latter (hereby *Zr-benefits*, *Zr-condition*, etc.). We then were able to perform

301 meta-regressions to verify how the strength of sexual selection on a putative sexual signal

302   (i.e. Zr-attractiveness) relates to the strength of the association between the conspicuousness

303   of that putative sexual signal and either benefits (Zr-benefits), individual condition (Zr-

304   condition), or other traits (Zr-size, Zr-dominance, Zr-sperm, Zr-age).

305   We found that sexual selection on putative sexual signal conspicuousness is positively

306   associated with the relationship between putative sexual signal conspicuousness and both the

307   benefits they provide (Fig. 5A; Fig. S3A) and bearers' individual condition (Fig. 5B; Fig.

308   S3B; Table S8). However, we found no evidence that sexual selection on putative sexual

309   signal conspicuousness is associated with the relationship between putative sexual signal

310   conspicuousness and other traits (Fig. 5C-F; Fig. S3C-E; Table S8). Nonetheless, data for

311   these analyses were scarce (Table S8), so these results require extra caution as they might not

312   be generalisable.

313   Theory predicts that mate choosiness, and thus pre-copulatory sexual selection,

314   increases with variation in mate quality[52,53]. Therefore, the positive relationship we found

315   between Zr-attractiveness and Zr-benefits is expected, but what about other variables? It

316   seems plausible that greater sexual selection on conspicuousness intensifies its condition-

317   dependence as an escalation of honest signalling (generating the positive relationship

318   between Zr-attractiveness and Zr-condition we found). By contrast, the relationship between

319   conspicuousness and other traits might be more variable because greater body size, social

320   dominance, expression of traits related to sperm competition, and age may lead to benefits to

321   their bearers only in certain situations. Perhaps the most valuable insight from these results is

322   that even when Zr-attractiveness is zero or negative (representing mate preference for lower

323   conspicuousness), other relationships between conspicuousness and distinct variables (e.g.

324   Zr-benefits, Zr-condition) can be positive (and vice-versa). This means that researchers

325   should not assume that positive relationships between putative sexual signal conspicuousness

326   and different variables attest that they are, indeed, sexually selected.

327

Future opportunities for research on putative sexual signals

329   Given that the relationship between the conspicuousness of putative sexual signals and

330   attractiveness to mates represents the core of the theory on mate choice, and that our dataset

331   represents the information collected by most meta-analyses on putative sexual signals, it is

332   astonishing that this relationship was available for only a quarter of the species (Fig. 2) and

333   represented less than 8% of all effect sizes in our dataset. The scarcity of data on

334   attractiveness suggests that biologists may inspect associations between conspicuous traits

335   and their potential benefits or costs without attesting to the attractive function of these traits

336   in the first place. However, we remind researchers that conspicuous traits can serve purposes

337   other than mate attraction, such as to signal status to conspecifics regardless of sex (see

338   previous sections), to deter[83] or confuse[84,85] predators, or to avoid sexual harassment[86].

339   Therefore, it is imperative to first examine the primary function of conspicuous traits, as

340   making assumptions about them can hamper our knowledge about their evolution. In fact, our

341   findings that signals under stronger mate choice are more strongly associated with benefits

342   they provide and with their condition-dependence suggest that the relationships we assessed

343   throughout our study (i.e. between putative sexual signals and benefits, condition, and traits)

344   should be much stronger if we could identify and select only the signals that are truly

345   attractive to mates.

346   In addition to the paucity of information related to the attractiveness of conspicuous

347   traits, our dataset contains other limitations inherited from the primary meta-analyses that we

348   used as sources, which largely represent deficits in the literature on sexual selection[4]. More

349   specifically, half of the species in our dataset are birds (Fig. 2) as most meta-analyses that we

350   collected data from focus on bird colouration (e.g. refs. [8–10,13–16,19,20,25,28,29,32,37,38,42,43,45,48]),

351   resulting in a dataset where other traits and animal groups (e.g. invertebrates) are

352 underrepresented (Figs. S4 and S5). Notably, female behaviours as putative sexual signals

353 were almost absent from our dataset despite being ubiquitous in nature (e.g. pheromones[87])

354 and potentially subjected to sexual selection[88], possibly leading to similar patterns to the ones

355 we found for other putative sexual signals (e.g. condition-dependence[89]). Although more data

356 may have become available after the primary meta-analyses we used as data sources were

357 published (i.e. data not included in our dataset), information on female behavioural sexual

358 signals and other neglected topics likely remains scarce. Collecting data on overlooked traits

359 and taxa should address these gaps and may even challenge our perceptions, such as of

360 stereotypical sex roles[90–92]. However, stronger incentives may be necessary to achieve this

361 goal[4].

362   While our study represents a solid advancement for the theory of sexual selection by

363 testing many of its predictions, and most of our results appear generalisable across taxa, we

364 stress that conspicuous traits in nature are extremely diverse. This means that existing and

365 future primary studies and meta-analyses on sexual signals remain valuable if they provide

366 in-depth investigations on factors that are unique to certain conspicuous traits (e.g. type of

367 pigment for colourful traits[48]). More importantly, the diversity we see in nature reinforces the

368 urgency in acquiring data beyond certain conspicuous traits and taxonomic groups. Failing to

369 do so risks leaving us with biassed and stagnant evidence, dimming the spark that Darwin

370 ignited over 150 years ago.

371

372 **Material and Methods**

373 *General*

374 Our methodology was described in our pre-registration[93] and in a twin study that essentially

375 used the same dataset as we did in the present study[94]. We report author contributions using

376 MeRIT guidelines[95] and the CRediT statement[96].

377

Deviations from the pre-registration

We planned to use the modality of putative sexual signals (i.e. whether they were visual,

acoustic, or other types of signals) as a moderator in meta-analytical models but we preferred

not to proceed with this decision because this variable overlapped with trait type (e.g. most

fixed putative sexual signals were visual traits). We did not verify the effect of re-extracted

vs. originally reported data as our related study using the same dataset showed that data

replicability was high[94]. PP adjusted variables within our framework from our pre-registration

(compare Table S1 with Table 1 from ref. [93], see also ref. [94]).

Putative sexual signal conspicuousness and variables within our framework

Our dataset contains information on the relationship between putative sexual signal

conspicuousness and many variables (Table S1; Fig. 1). To clarify, putative sexual signals

refer to traits thought to be involved in mate attraction (by authors of empirical papers or of

primary meta-analyses that we used as data sources, see next section; weapons or body size

were not considered valid putative sexual signals; see also ref. [97]). On the other hand,

conspicuousness refers to the expected direction of attractiveness to mates regarding the

expression of putative sexual signals. For instance, more colourful traits are expected to be

more attractive, and thus greater values of certain colour metrics that reflect this (e.g.

chroma) are deemed more conspicuous. However, despite using conspicuousness throughout

the manuscript for all putative sexual signals, other terms could be more appropriate in many

cases. For example, more symmetric traits are often expected to be more appealing to mates,

so they were deemed more conspicuous, even though this term may be misleading here.

Conspicuousness for other putative sexual signals may be even more confusing as the

expectations on the direction of their appeal is expected to differ across taxa or scenarios, e.g.

402   sounds with higher frequency are expected to be more appealing for birds[11] but less appealing

403   for amphibians[21]. PP ascertained the expected direction of attractiveness (i.e.

404   conspicuousness) based on information provided by authors of empirical and primary meta-

405   analyses (see Table S2) but we note that what is considered more appealing to mates

406   according to these authors has often not been tested. In fact, PP was not able to infer the

407   expected direction of attractiveness for certain traits when we directly extracted data from

408   empirical studies. PP then made additional analyses (see below) in which effect sizes with

409   ambiguous direction were removed or changed to their opposite value to ensure our results

410   were robust (see Table S3).

411   Variables within our framework are explained throughout the manuscript as results are

412   reported, while their direction and more examples are given in Table S1. Meta-analyses'

413   authors were often vague regarding the exact data they extracted, so interconnected proxies,

414   such as reproductive success and viability measures, were difficult to separate. For instance,

415   whether "fledgling success" means number of fledglings (reproductive success) or proportion

416   of offspring that fledged from all eggs laid (viability) was unclear in many cases, so PP

417   deemed most of them as reproductive success given that this is a more diverse measure.

418

419   *Data collection*

420   As previously stated, our data collection is fully reported in ref. [94]. Briefly, PP compiled

421   individual effect sizes from 41 primary meta-analyses[7–21,24–49], which contained relevant data

422   for our study from 1,196 empirical sources. Then, all authors (re-)extracted all data related to

423   putative sexual signals from 243 empirical studies [54–56,98–340] that these meta-analyses used as

424   sources. Most of these studies were selected because multiple meta-analyses used them and

425   produced mismatching individual effect sizes [94]. This process was done as part of a

426   reproducibility and replicability project[94] but also provided the base to the present study as it

427 essentially deduplicated and ensured the quality of our dataset (see below). After data re-

428 extractions, PP replaced the individual effect sizes reported by meta-analyses with re-

429 extracted effect sizes for these 243 empirical studies. Other effect sizes reported by meta-

430 analyses (from empirical studies whose data we did not re-extract) were maintained in the

431 dataset. Despite these 243 empirical studies being cited as data sources by meta-analyses,

432 many of the effect sizes re-extracted by us were not actually reported by primary meta-

433 analyses or, alternatively, were reported by primary meta-analyses with a different value from

434 the ones we obtained during re-extraction (see ref. [94]). Thus, to some extent, our dataset

435 contains data that have not been used in previous meta-analyses. PP additionally removed

436 identically reported effect sizes (both in description and in value) from other duplicated

437 empirical studies (those that we did not extract data from). This process ensured that all

438 individual effect sizes in our dataset were unique, in contrast to meta-meta-analyses that

439 analyse mean effect sizes from primary meta-analyses (e.g. refs. [341–343]), which can

440 encompass repeated data (as the same empirical studies can be used by multiple primary

441 meta-analyses). PP further removed from the dataset data that were unfit to verify the

442 relationship between putative sexual signal conspicuousness and distinct variables, such as

443 measurements of parental care after manipulation of putative sexual signals (e.g. ref. [236]).

444 After these procedures, our dataset tallied 7,428 effect sizes, with 4,237 of them (57% of the

445 dataset) being extracted by us and the remaining effect sizes being originally reported by

446 primary meta-analyses[7–21,24–49]. We used Fisher's Zr as our effect size, transforming it to

447 correlation coefficient (r) when reporting most of our results. Details on the calculation of

448 effect sizes, including all equations used, are reported in ref. [94].

449

450 *Analyses*

451   PP constructed separate meta-analytical models to verify the relationship between putative

452   sexual signal conspicuousness and each variable within our framework, resulting in seven

453   sets of models (one set for each background colour in Figs. 3 and 4). PP used multilevel

454   meta-analytical models because effect sizes were not independent of one another. Different

455   effect sizes could share the same (empirical) study ID, species ID, and trait type ID (i.e.

456   flexible or fixed trait, nested within-species). Thus, in addition to effect size ID, PP used

457   these variables as random factors in our models to control for non-independence. PP also

458   included a correlation matrix related to phylogenetic relatedness for the species in our model

459   as a random factor[344]. From meta-analytical models with all these random factors, PP

460   quantified I^2_{total} (a measure of heterogeneity not attributed to sampling error[345]) and how

461   much of it each random factor explained (partial I^2; see Table S4). PP fitted meta-analytical

462   models with the following fixed factors: none (only intercept, showing the average

463   relationship), sub variable (only models involving benefits and individual condition, see

464   Table S1), sex (male, female, or unknown) and trait type (fixed or flexible). PP followed ref.

465   [346] to interpret the magnitude to mean effect sizes (as Zr, before converting them to r, "weak"

466   for values up to 0.2, "moderate" for values up to 0.5, and "high" for greater values).

467   PP also constructed additional versions of all models described above, in which we

468   removed or inverted the value of data points whose direction was ambiguous (e.g. putative

469   sexual signals without information on expected direction for mate attraction or data with

470   direction not clearly reported in empirical studies). The results of these analyses were very

471   similar to the ones with data points as originally extracted (Table S3).

472   We tested for signs of publication bias in meta-analytical models using three

473   approaches (see Table S7, Figs. S1 and S2). First, we visually evaluated funnel asymmetry

474   for each model using funnel plots, which show the residuals of meta-analytical models

475   containing all moderators against effect sizes' precision (i.e. inverse of standard error).

476 Second, we further assessed funnel asymmetry with an alternative approach to Egger's

477 regression: using the inverse of the effective sample size as a moderator in a multilevel meta-

478 analytical model [347]. Third, in the same meta-analytical models of the second approach, we

479 verified time-lag bias using publication year as a moderator[348].

480   To verify whether the relationship between putative sexual signal conspicuousness

481 and attractiveness is associated with the relationship between putative sexual signal

482 conspicuousness and other variables within our framework, we sought conspicuous traits in

483 our dataset with both of these relationships. We used two approaches to collect and link these

484 data. In the first approach (hereby *across-studies*, Fig. 5), we calculated a mean effect size for

485 each putative sexual signal (across different empirical studies examining a given species)

486 regarding the relationship between its conspicuousness and attractiveness to mates (Zr-

487 attractiveness). We then linked these estimates to mean effect sizes regarding the relationship

488 between the conspicuousness of that same putative sexual signal and another variable (Zr-

489 benefits, Zr-condition, etc.), also across different empirical studies examining a given species.

490 This first approach assumes that the relationship between attractiveness and putative sexual

491 conspicuousness across time and populations is consistent, which is not necessarily true[349].

492 To ameliorate this issue, our second approach (hereby *within-studies*; Fig. S3) only links

493 these relationships (Zr-attractiveness with either Zr-benefits, Zr-condition, Zr-size, Zr-

494 dominance, Zr-sperm, or Zr-age) extracted from the same empirical study. This second

495 approach is more reliable but yields fewer data points, such that the relationship between Zr-

496 attractiveness and Zr-sperm could not be analysed with this second approach as a single data

497 point was available. We only show the results of the first approach in the manuscript as both

498 approaches generated similar qualitative results.

499   Meta-regressions described above accounted for the variation of effect sizes serving

500 as the response variables (i.e. Zr-benefits, Zr-condition, etc.), but disregarded the dispersal of

501 effect sizes serving as predictor variables (i.e. Zr-attractiveness). In other words, they are

502 univariate models. To correct this, we conducted bivariate models, in which the dispersal of

503 both response and predictor variables is considered. However, this approach yields much

504 larger confidence intervals and estimates generated may not be reliable as we could not

505 preclude divergent transitions when running these analyses. Thus, we preferred to show

506 results of only univariate models (with the across-studies approach) in the manuscript, but

507 results for other approaches and models can be found in Table S8.

508 All statistical analyses were conducted in the software R 4.4.0[350]. We fitted meta-

509 analytical models (except for bivariate models) using the *rma.mv* function from the package

510 *metafor*[351]. Bivariate models were fitted using the package *brms*[352], in which we ran three

511 chains, each with 10,000 iterations plus another 10,000 burn-in iterations. In these analyses,

512 we adopted Stan's standard uninformative priors, and set the maximum tree depth to 12 and

513 the adaptive delta to 0.999. We calculated R^2 [353] and I^2 using, respectively, the *r2_ml* and

514 *i2_ml* function from the package *orchaRd*[354]. Phylogenetic trees were built using the

515 packages *ape*[355] and *rotl*[356]. We performed pairwise comparisons (two-tailed z-tests) using the

516 function *glht* from the package *multcomp*[357].

517

531 **Author contributions**

532 Conceptualisation: PP, ML, RCMR, AM, YY, SN

533 Data curation: PP

534 Formal analysis: PP

535 Funding acquisition: SN

536 Investigation: PP, ML, RCMR, AM, YY, SN

537 Methodology: PP, SN

538 Project administration: PP

539 Software: PP

540 Supervision: SN

541 Visualisation: PP

542 Writing – original draft: PP, SN

543 Writing – review & editing: PP, ML, RCMR, AM, YY, SN.

544

545 **Competing interests**

546 We declare no competing interests.

547

548 **Data and code availability**

549   All data and code used in this study are available at:

550   https://osf.io/6njem/?view_only=7b01538fb32e4f78b7130b6e8f303649.

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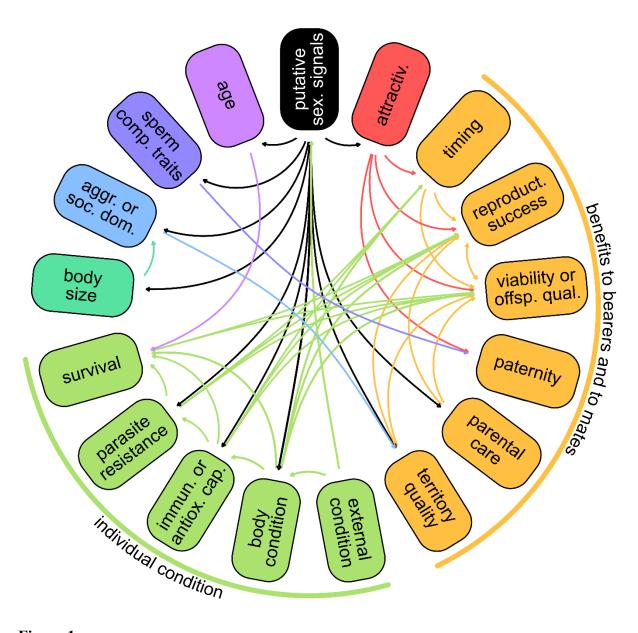
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Figures

Figure 1.

Framework for the relationship between putative sexual signals and different variables

(clockwise from the top): conspicuousness of putative sexual signals, attractiveness, benefits

to bearers and to mates (timing, reproductive success, viability or offspring quality, paternity,

parental care, territory quality), individual condition (external condition, body condition,

immunological or antioxidant capacity, parasite resistance, survival), body size, aggression or

social dominance, traits related to sperm competition, and age (see also Table S1). Arrows

1431   represent that a variable potentially influences or signals another variable (see text for
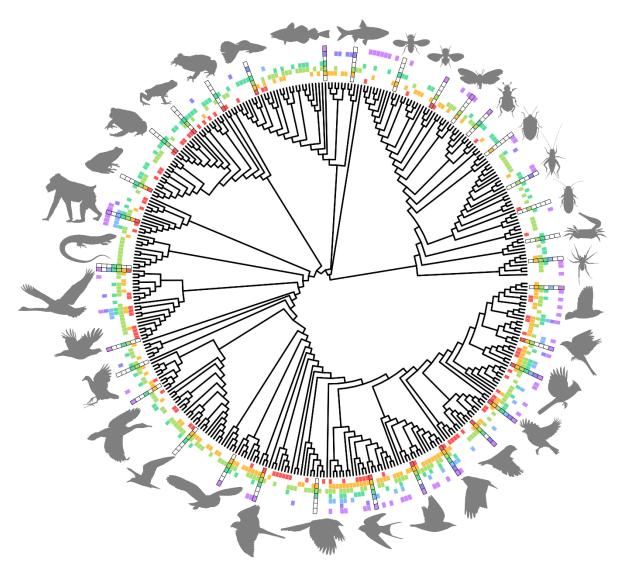
1432   details).

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1434

Figure 2.

Phylogeny of the 375 animal species present in our dataset. Each ring around the

phylogenetic tree indicates the existence (colourful cells) or absence (blank cells) of data on

the relationship between the conspicuousness of one or more putative sexual signals of a

given species and a variable assessed in our study (red: attractiveness, orange: benefits to

bearers and to mates, green: individual condition, aquamarine: body size, blue: aggression or

social dominance, indigo: traits related to sperm competition, violet: age). Silhouettes

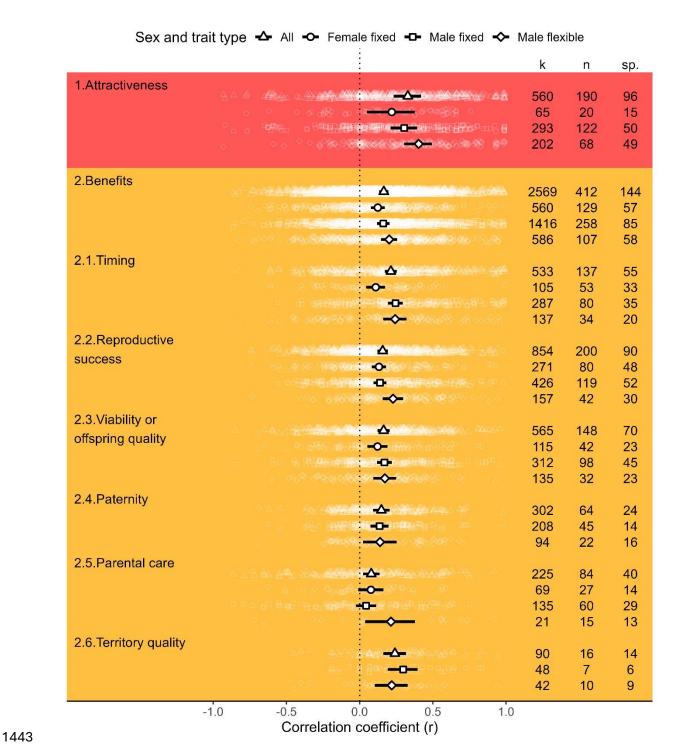represent species whose nearby cells have black edges.

Figure 3.

Mean effect sizes for relationship between the conspicuousness of putative sexual signals and their bearers' attractiveness (red zone) and benefits (to bearers and to their mates; orange zone). Variance explained by fixed factors in these models (marginal R^2) were, respectively, 2.3% and 4.1% (see Table S6). The vertical black dotted line highlights zero (no relationship).

1449   k, n, and sp. represent, respectively, the number of effect sizes, empirical studies, and species
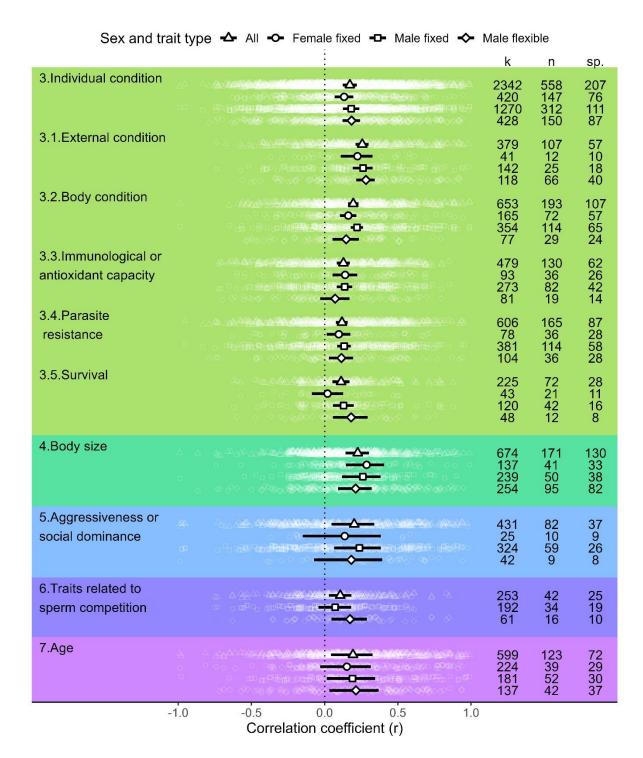
1450   for each set.

Figure 4.

Mean effect sizes for the relationship between the conspicuousness of putative sexual signals and their bearers' condition, body size, aggressiveness or social dominance, traits related to sperm competition, or age. Variance explained by fixed factors in these models (marginal R^2)

1456   were, respectively, 4.9%, 1.2%, 1.9%, 3.3%, and 0.5% (see Table S6). k, n, and sp. represent,

1457   respectively, the number of effect sizes, empirical studies, and species for each set.
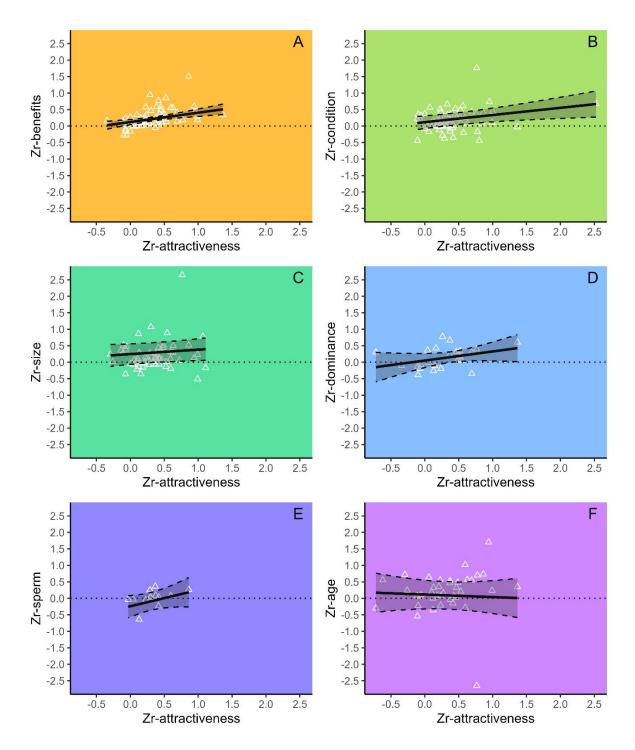
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Figure 5.

Meta-regressions between two relationships: putative sexual signal conspicuousness and

attractiveness to mates (x-axis, i.e. Zr-attractiveness) and putative sexual signal

conspicuousness and other variables from our framework (y-axis; A: benefits, B: individual

condition, C: body size, D: aggression or social dominance, E: traits related to sperm

1464   competition, F: age). Solid lines represent slopes, hashed areas between dashed lines

1465   represent slopes' 95% confidence interval, and dotted lines highlight zero.
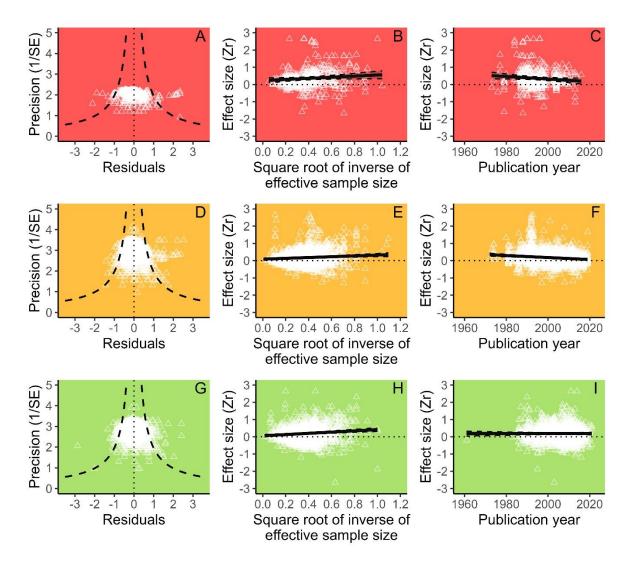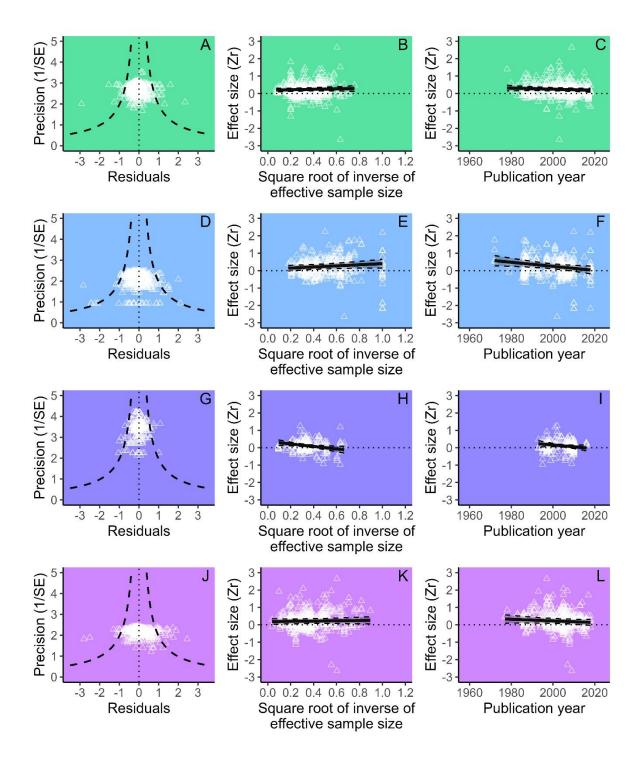
Supplementary material

Figure S1.

Assessments of publication bias: funnel plots of the residuals of meta-analytical models with

all moderators used (1st column), relationship between effect size (Zr) and square root of

inverse of effective sample size (2nd column), and relationship between effect size (Zr) and

publication year (3rd column). Dashed lines represent 95% confidence intervals for expected

values (1st column) or for regression estimates (2nd and 3rd columns). Panels refer to

attractiveness (A-C), benefits (D-F), or individual condition (G-I).

1475

Figure S2.

Assessments of publication bias: funnel plots of the residuals of meta-analytical models with all moderators used (A, D, G, J), relationship between effect size (Zr) and square root of inverse of effective sample size (B, E, H, K), and relationship between effect size (Zr) and publication year (C, F, I, L). Dashed lines represent 95% confidence intervals for expected

1481   values (A, D, G, J) or for regression estimates (B, C, E, F, H, I, K, L). Panels refer to body

1482   size (A-C), aggressiveness or social dominance (D-F), traits related to sperm competition (G-

1483   I), or age (J-L).

1484

Figure S3.

Meta-regressions between two relationships (considering only information from the same

study, i.e. within-study approach): putative sexual signal conspicuousness and attractiveness

to mates (x-axis, i.e. Zr-attractiveness) and putative sexual signal conspicuousness and other

variables from our framework (y-axis; A: benefits, B: individual condition, C: body size, D:

1490   aggression of social dominance, E: age). Solid lines represent slopes, hashed areas between

1491   dashed lines represent slopes' 95% confidence interval, and dotted lines highlight zero.

1492

Figure S4.

Proportion (x-axis) and number (inside bars) of species for which we had information on the relationship between putative sexual signal conspicuousness and several variables (y-axis) assessed in our study, for each sex (left panel) and trait type (right panel).

Figure S5.

Proportion (x-axis) and number (inside bars) of effect sizes for which we had information on the relationship between putative sexual signal conspicuousness and several variables (y-axis) assessed in our study, for each sex (left panel) and trait type (right panel).
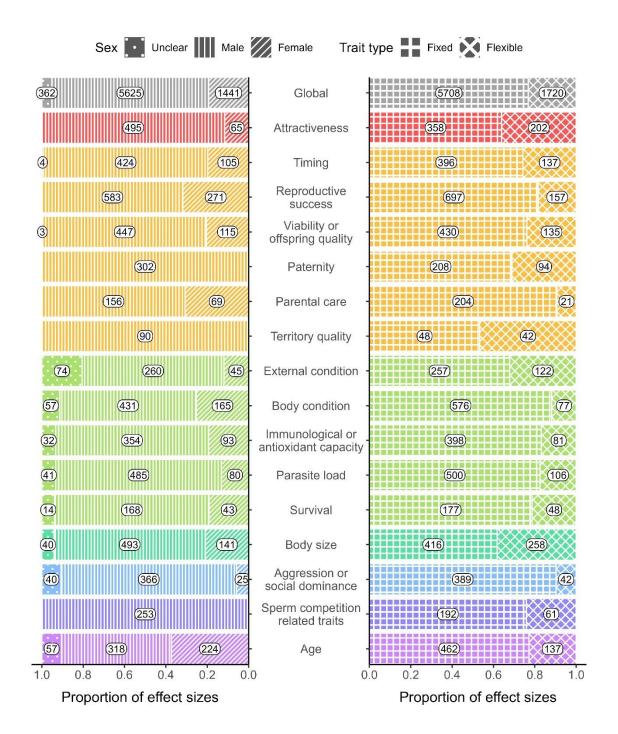
1503 **Table S1.**

1504 Variables within our framework, for which we verified the relationship with putative sexual

1505 signal conspicuousness. *N* represents the number of primary meta-analyses in our dataset that

1506 explored these variables. Underlined examples are predicted to have a negative relationship

1507 with sexual signal conspicuousness, while others are predicted to have a positive relationship

1508 with sexual signal conspicuousness.

1509

Variable	Sub variable	*N*	Examples
Attractiveness	-	15	Copulation success, harem size, success in mate choice trials, <u>divorce</u>, pairing success or status
Benefits to sexual signal bearers or to their mates	Timing	9	<u>Latency to arrive at breeding site</u>, <u>latency to nest</u>, <u>latency to pair</u>, <u>latency to mate</u>, <u>latency to breed</u>, <u>latency to lay eggs</u>, <u>latency for eggs to hatch</u>, <u>latency for offspring to fledge</u>
	Reproductive success	12	Clutch size, breeding success, number of fledglings, total offspring sired, number of recruits
	Offspring quality or viability	9	Antioxidants or hormones in yolk, offspring growth rate, offspring attractiveness, offspring reproductive success, proportion of eggs hatched, fledging success, offspring size
	Paternity	10	Within and extra-pair paternity, <u>cuckoldry occurrence</u>
	Parental care	7	Feeding rate, incubation frequency
	Territory	2	Territory quality or size
Individual condition	External condition	7	<u>Increase in brood size or reproductive effort</u>, decrease in brood size or reproductive effort, habitat quality, mother's condition, <u>date when reared</u>, diet supplementation, <u>dietary deprivation</u>, <u>nutritional stress</u>
	Body condition	11	Carotenoid, protein, or lipid amount in plasma or in feathers, unspecified body condition, feather quality, subcutaneous fat score, residual mass, pectoral score
	Immune or antioxidant capacity	10	Antibody response, <u>glucocorticoids</u>, hematocrit, <u>heterophil-to-lymphocyte ratio</u>, <u>oxidative damage</u>, white blood cells
	Parasite resistance	10	<u>Abundance of parasites</u>, <u>infection with a pathogen</u>, <u>pathogen richness</u>, parasite removal
	Survival	9	Days alive, seen or re-captured after a given period
Body size	-	8	Body (or part of it) mass, length, width, depth, area, or volume
Aggression or social dominance	-	7	Performed aggression, <u>received aggression</u>, dominance, fights initiated, social rank, nest defence, <u>distance from intruder</u>, territory tenure
Traits related to sperm competition	-	1	Quantity of seminal fluid, sperm size, sperm viability, testes size
Age	-	8	Age, ontogenetic stage (e.g. adult *vs*. juvenile)

1510

1511 **Table S2.**

1512 Presumed directionality of conspicuousness among various putative sexual signals.

1513

Trait type	Trait description	Conspicuousness direction
Fixed	Colour, brightness	Often positive but negative in some cases (e.g. some melanin-based traits)
	Colour, chroma or saturation	Often positive but negative in some cases (e.g. some melanin-based traits)
	Colour, hue	Often positive but negative in some cases (e.g. blue traits)
	Colour, others (e.g. discrete ratings)	Case-dependent
	Size	Positive
	Symmetry	Positive
Flexible	Display duration	Positive
	Display vigour	Positive
	Latency to display	Negative
	Number of displays	Positive
	Repertoire size	Positive
	Sound amplitude	Positive
	Sound frequency	Often positive but negative in some cases (e.g. amphibians)
	Symmetry of extended phenotype (e.g. bowers)	Positive
	Other properties	Case-dependent

1514

Table S3.

Estimated correlation coefficients from meta-analytical models. Three types of analyses are

reported regarding how we dealt with data points with ambiguous direction: (1) "original"

refers to results reported in the manuscript, which used data points as originally extracted; (2)

"opposite" instead uses the opposite value of these data points; (3) "removed" refers to

analyses without these data points.

Variable	Sub variable	Set	Analysis	Estimate	Standard error	95%CI lower bound	95%CI upper bound
Attractiveness	-	All	Original	0.329	0.053	0.233	0.419
			Opposite	0.330	0.054	0.233	0.420
			Removed	0.333	0.054	0.235	0.423
		Female fixed	Original	0.220	0.088	0.050	0.377
			Opposite	0.234	0.090	0.062	0.393
			Removed	0.226	0.089	0.054	0.385
		Male fixed	Original	0.304	0.051	0.211	0.392
			Opposite	0.306	0.053	0.208	0.397
			Removed	0.309	0.053	0.212	0.400
		Male flexible	Original	0.403	0.057	0.304	0.493
			Opposite	0.394	0.060	0.291	0.488
			Removed	0.402	0.059	0.299	0.495
Benefits to sexual signal bearers or to their mates	-	All	Original	0.165	0.017	0.133	0.197
			Opposite	0.158	0.017	0.125	0.191
			Removed	0.170	0.017	0.137	0.203
		Female fixed	Original	0.124	0.025	0.077	0.171
			Opposite	0.126	0.029	0.070	0.181
			Removed	0.133	0.026	0.084	0.182
		Male fixed	Original	0.161	0.022	0.118	0.204
			Opposite	0.155	0.027	0.103	0.206
			Removed	0.164	0.023	0.120	0.208
		Male flexible	Original	0.202	0.029	0.146	0.257
			Opposite	0.194	0.033	0.131	0.256
			Removed	0.209	0.031	0.152	0.266
	Timing	All	Original	0.213	0.022	0.171	0.254
			Opposite	0.223	0.023	0.181	0.265
			Removed	0.219	0.023	0.176	0.262
		Female fixed	Original	0.110	0.033	0.045	0.174
			Opposite	0.144	0.034	0.079	0.209
			Removed	0.126	0.035	0.059	0.193
		Male fixed	Original	0.245	0.028	0.194	0.295
			Opposite	0.254	0.028	0.201	0.305
			Removed	0.242	0.028	0.190	0.294
			Original	0.242	0.043	0.161	0.320

	Male flexible	Opposite	0.219	0.044	0.136	0.300
		Removed	0.247	0.044	0.165	0.326
Reproductive success	All	Original	0.157	0.019	0.121	0.193
		Opposite	0.152	0.019	0.115	0.189
		Removed	0.166	0.020	0.128	0.203
	Female fixed	Original	0.132	0.025	0.084	0.180
		Opposite	0.134	0.026	0.084	0.183
		Removed	0.140	0.026	0.089	0.190
	Male fixed	Original	0.139	0.023	0.094	0.183
		Opposite	0.131	0.024	0.085	0.176
		Removed	0.142	0.024	0.097	0.188
	Male flexible	Original	0.228	0.038	0.157	0.297
		Opposite	0.224	0.038	0.152	0.295
		Removed	0.245	0.039	0.172	0.315
Offspring quality or viability	All	Original	0.164	0.022	0.123	0.205
		Opposite	0.149	0.022	0.106	0.190
		Removed	0.171	0.022	0.128	0.214
	Female fixed	Original	0.122	0.036	0.053	0.190
		Opposite	0.107	0.036	0.037	0.177
		Removed	0.132	0.038	0.058	0.204
	Male fixed	Original	0.170	0.026	0.119	0.219
		Opposite	0.155	0.027	0.103	0.206
		Removed	0.178	0.027	0.127	0.229
	Male flexible	Original	0.172	0.041	0.093	0.250
		Opposite	0.157	0.042	0.075	0.236
		Removed	0.171	0.043	0.088	0.252
Paternity	All	Original	0.149	0.029	0.092	0.204
		Opposite	0.143	0.030	0.085	0.199
		Removed	0.151	0.030	0.094	0.208
	Male fixed	Original	0.136	0.032	0.074	0.198
		Opposite	0.133	0.033	0.070	0.196
		Removed	0.136	0.032	0.073	0.197
	Male flexible	Original	0.140	0.060	0.022	0.253
		Opposite	0.119	0.062	-0.003	0.237
		Removed	0.140	0.061	0.022	0.254
Parental care	All	Original	0.079	0.029	0.022	0.136
		Opposite	0.052	0.030	-0.006	0.110
		Removed	0.069	0.031	0.008	0.130
	Female fixed	Original	0.077	0.044	-0.009	0.162
		Opposite	0.030	0.045	-0.057	0.117
		Removed	0.070	0.049	-0.025	0.164
	Male fixed	Original	0.044	0.036	-0.026	0.113
		Opposite	0.020	0.036	-0.051	0.091
		Removed	0.027	0.037	-0.046	0.100
	Male flexible	Original	0.214	0.092	0.037	0.378
		Opposite	0.248	0.092	0.071	0.409
		Removed	0.253	0.095	0.072	0.418
Territory	All	Original	0.241	0.042	0.162	0.317
		Opposite	0.241	0.043	0.161	0.318
		Removed	0.236	0.043	0.156	0.314

Individual condition				Value 1	Value 2	Value 3	Value 4
		Male fixed	Original	0.298	0.057	0.192	0.397
			Opposite	0.300	0.058	0.193	0.400
			Removed	0.285	0.058	0.176	0.387
		Male flexible	Original	0.219	0.060	0.104	0.329
			Opposite	0.213	0.061	0.096	0.324
			Removed	0.229	0.061	0.113	0.338
	-	All	Original	0.174	0.026	0.124	0.224
			Opposite	0.174	0.027	0.121	0.225
			Removed	0.177	0.026	0.128	0.226
		Female fixed	Original	0.134	0.034	0.069	0.198
			Opposite	0.137	0.035	0.070	0.203
			Removed	0.137	0.034	0.072	0.201
		Male fixed	Original	0.184	0.030	0.126	0.241
			Opposite	0.182	0.032	0.121	0.241
			Removed	0.187	0.030	0.129	0.244
		Male flexible	Original	0.186	0.033	0.123	0.247
			Opposite	0.184	0.034	0.119	0.248
			Removed	0.186	0.033	0.124	0.248
	External condition	All	Original	0.263	0.026	0.215	0.310
			Opposite	0.265	0.029	0.211	0.318
			Removed	0.274	0.028	0.222	0.325
		Female fixed	Original	0.228	0.062	0.110	0.339
			Opposite	0.222	0.062	0.104	0.334
			Removed	0.227	0.065	0.104	0.343
		Male fixed	Original	0.269	0.041	0.194	0.341
			Opposite	0.278	0.041	0.203	0.350
			Removed	0.289	0.043	0.210	0.364
		Male flexible	Original	0.290	0.038	0.219	0.357
			Opposite	0.293	0.039	0.222	0.360
			Removed	0.296	0.039	0.226	0.364
Individual condition	Body condition	All	Original	0.198	0.020	0.161	0.235
			Opposite	0.199	0.024	0.153	0.244
			Removed	0.202	0.022	0.160	0.244
		Female fixed	Original	0.163	0.030	0.105	0.220
			Opposite	0.171	0.030	0.113	0.228
			Removed	0.168	0.031	0.108	0.227
		Male fixed	Original	0.225	0.024	0.180	0.269
			Opposite	0.220	0.024	0.175	0.265
			Removed	0.228	0.025	0.181	0.273
		Male flexible	Original	0.148	0.048	0.054	0.238
			Opposite	0.147	0.049	0.053	0.239
			Removed	0.145	0.049	0.051	0.237
	Immune or antioxidant capacity	All	Original	0.129	0.023	0.084	0.174
			Opposite	0.126	0.028	0.073	0.179
			Removed	0.128	0.026	0.078	0.178
		Female fixed	Original	0.141	0.045	0.054	0.227
			Opposite	0.142	0.045	0.054	0.228
			Removed	0.144	0.046	0.056	0.230
		Male fixed	Original	0.138	0.028	0.084	0.191
			Opposite	0.135	0.028	0.081	0.189

			Removed	0.140	0.029	0.084	0.195
		Male flexible	Original	0.072	0.052	-0.030	0.172
			Opposite	0.081	0.053	-0.022	0.182
			Removed	0.073	0.053	-0.030	0.175
Parasite resistance		All	Original	0.119	0.021	0.078	0.159
			Opposite	0.123	0.025	0.074	0.171
			Removed	0.128	0.023	0.082	0.172
		Female fixed	Original	0.097	0.042	0.015	0.178
			Opposite	0.108	0.042	0.025	0.189
			Removed	0.110	0.044	0.023	0.195
		Male fixed	Original	0.134	0.025	0.086	0.181
			Opposite	0.136	0.025	0.088	0.183
			Removed	0.141	0.025	0.092	0.189
		Male flexible	Original	0.115	0.043	0.030	0.197
			Opposite	0.100	0.044	0.015	0.184
			Removed	0.111	0.044	0.026	0.196
Survival		All	Original	0.113	0.031	0.053	0.172
			Opposite	0.100	0.034	0.034	0.166
			Removed	0.108	0.033	0.044	0.172
		Female fixed	Original	0.020	0.055	-0.088	0.127
			Opposite	0.003	0.055	-0.105	0.111
			Removed	0.013	0.057	-0.098	0.123
		Male fixed	Original	0.130	0.038	0.057	0.202
			Opposite	0.125	0.038	0.051	0.197
			Removed	0.133	0.039	0.058	0.206
		Male flexible	Original	0.183	0.065	0.057	0.302
			Opposite	0.147	0.066	0.019	0.271
			Removed	0.162	0.066	0.033	0.286
Body size	-	All	Original	0.230	0.045	0.144	0.312
			Opposite	0.228	0.051	0.132	0.319
			Removed	0.232	0.041	0.155	0.307
		Female fixed	Original	0.295	0.080	0.147	0.431
			Opposite	0.297	0.084	0.140	0.440
			Removed	0.295	0.077	0.152	0.426
		Male fixed	Original	0.267	0.078	0.119	0.403
			Opposite	0.269	0.083	0.113	0.413
			Removed	0.262	0.075	0.120	0.394
		Male flexible	Original	0.215	0.065	0.092	0.333
			Opposite	0.212	0.069	0.079	0.337
			Removed	0.221	0.061	0.105	0.331
Aggression or social dominance	-	All	Original	0.205	0.082	0.047	0.354
			Opposite	0.202	0.087	0.034	0.358
			Removed	0.206	0.084	0.044	0.358
		Female fixed	Original	0.138	0.147	-0.151	0.404
			Opposite	0.114	0.147	-0.174	0.383
			Removed	0.131	0.148	-0.159	0.401
		Male fixed	Original	0.242	0.092	0.065	0.404
			Opposite	0.245	0.095	0.064	0.410
			Removed	0.245	0.093	0.066	0.409
			Original	0.184	0.131	-0.072	0.416

		Male flexible	Opposite	0.188	0.130	-0.066	0.420
			Removed	0.189	0.130	-0.064	0.419
Traits related to sperm competition	-	All	Original	0.107	0.040	0.029	0.185
			Opposite	0.103	0.044	0.017	0.188
			Removed	0.108	0.040	0.031	0.184
		Male fixed	Original	0.072	0.058	-0.043	0.184
			Opposite	0.068	0.059	-0.048	0.183
			Removed	0.072	0.058	-0.042	0.185
		Male flexible	Original	0.175	0.066	0.046	0.297
			Opposite	0.170	0.067	0.041	0.294
			Removed	0.176	0.066	0.047	0.299
Age	-	All	Original	0.196	0.079	0.043	0.340
			Opposite	0.201	0.054	0.099	0.300
			Removed	0.197	0.085	0.032	0.350
		Female fixed	Original	0.153	0.094	-0.030	0.326
			Opposite	0.174	0.075	0.028	0.313
			Removed	0.163	0.100	-0.032	0.346
		Male fixed	Original	0.193	0.092	0.014	0.360
			Opposite	0.208	0.074	0.067	0.342
			Removed	0.203	0.098	0.013	0.380
		Male flexible	Original	0.217	0.096	0.032	0.387
			Opposite	0.198	0.078	0.047	0.341
			Removed	0.206	0.102	0.009	0.388

1522

Table S4.

Heterogeneity (I^2) observed in meta-analytical models on the relationship between the

expression of putative sexual signals and different variables within our framework.

Variable	I^2_{total}	$I^2_{within\text{-}study}$ (effect size ID)	$I^2_{across\text{-}study}$ (study ID)	$I^2_{across\text{-}species}$ (species ID)	$I^2_{phylogeny}$	$I^2_{within\text{-}species}$ trait type
Attractiveness	91.537	55.947	25.180	<0.001	2.252	8.158
Benefits to sexual signal bearers or to their mates	88.017	51.591	25.048	0.684	<0.001	10.694
Individual condition	85.176	52.427	26.649	4.778	1.321	<0.001
Body size	87.193	35.080	04.278	<0.001	3.599	44.236
Aggression or social dominance	78.527	19.885	43.136	9.353	5.237	0.916
Traits related to sperm competition	75.923	31.769	42.970	<0.001	1.183	0.000
Age	93.585	44.460	28.500	<0.001	7.395	13.230

1527

Table S5.

Pairwise comparisons (two-tailed test) among combinations of sex and trait type. Shaded

cells highlight significant comparisons (*p-value* < 0.05).

Variable	Sub variable	Female fixed *vs.* male fixed		Female fixed *vs.* male flexible		Male fixed *vs.* male flexible	
		z-value	*p-value*	*z-value*	*p-value*	*z-value*	*p-value*
Attractiveness	–	-1.048	0.294	-2.070	0.038	-1.735	0.083
Benefits to sexual signal bearers or to their mates	–	-2.068	0.039	-2.229	0.026	-1.227	0.220
	Timing	-3.975	<0.001	-2.538	0.011	0.058	0.954
	Reproductive success	-0.276	0.783	-2.214	0.027	-2.120	0.034
	Offspring quality or viability	-1.321	0.186	-0.949	0.343	-0.058	0.953
	Paternity	–	–	–	–	-0.050	0.960
	Parental care	0.664	0.507	-1.380	0.168	-1.774	0.076
	Territory	–	–	–	–	-1.024	0.306
Individual condition	–	-2.484	0.013	-1.662	0.097	-0.071	0.943
	External condition	-0.718	0.472	-0.924	0.356	-0.403	0.687
	Body condition	-2.060	0.039	0.283	0.777	1.540	0.124
	Immune or antioxidant capacity	0.075	0.941	1.046	0.295	1.213	0.225
	Parasite resistance	-0.851	0.395	-0.301	0.763	0.407	0.684
	Survival	-1.981	0.048	-1.983	0.047	-0.750	0.453
Body size	–	0.936	0.349	1.241	0.215	0.812	0.417
Aggression or social dominance	–	-0.710	0.478	-0.257	0.797	0.515	0.606
Traits related to sperm competition	–	–	–	–	–	-2.076	0.038
Age	–	-0.862	0.388	-0.701	0.484	-0.276	0.782

1532

1533 **Table S6.**

1534 Marginal R^2 (i.e. variation of data explained by fixed factors) and conditional R^2 (i.e.

1535 variation of data explained by random and fixed factors) of meta-analytical models on the

1536 relationship between putative sexual signal conspicuousness and different variables, with sub

1537 variable, sex, and trait type as fixed factors.

1538

Variable	Marginal R^2	Conditional R^2
Attractiveness	0.023	0.387
Benefits to sexual signal bearers or to their mates	0.041	0.400
Individual condition	0.049	0.395
Body size	0.012	0.617
Aggression or social dominance	0.019	0.742
Traits related to sperm competition	0.033	0.571
Age	0.005	0.537

1539

1540 **Table S7.**

1541 Results of meta-analytical models on the relationship between putative sexual signal

1542 conspicuousness and different variables, with the square root of the inverse of effective

1543 sample size (SIESS) and publication year of empirical sources as moderators. Positive

1544 estimates for SIESS indicate publication bias and negative estimates for publication year

1545 indicate time-lag publication bias (shaded rows highlight these cases when statistically

1546 significant).

1547

Variable	Term	Estimate	SE	z-value	p-value	95%CI
Attractiveness	Intercept	0.356	0.045	7.835	<0.001	0.267 to 0.442
	SIESS	0.056	0.028	1.948	0.051	-0.001 to 0.111
	Time-lag	-0.054	0.028	-1.937	0.053	-0.109 to 0.000
Benefits to sexual signal bearers or to their mates	Intercept	0.170	0.016	10.85	<0.001	0.140 to 0.201
	SIESS	0.033	0.010	3.444	0.001	0.014 to 0.052
	Time-lag	-0.052	0.012	-4.262	<0.001	-0.077 to -0.028
Individual condition	Intercept	0.187	0.027	6.910	<0.001	0.134 to 0.240
	SIESS	0.048	0.010	5.015	<0.001	0.029 to 0.066
	Time-lag	0.001	0.011	0.060	0.953	-0.021 to 0.023
Body size	Intercept	0.231	0.046	5.067	<0.001	0.142 to 0.321
	SIESS	0.016	0.018	0.894	0.372	-0.020 to 0.052
	Time-lag	-0.029	0.024	-1.200	0.230	-0.076 to 0.018
Aggression or social dominance	Intercept	0.244	0.073	3.326	0.001	0.100 to 0.388
	SIESS	0.063	0.036	1.752	0.080	-0.007 to 0.134
	Time-lag	-0.115	0.047	-2.465	0.014	-0.207 to -0.024
Traits related to sperm competition	Intercept	0.111	0.036	3.117	0.002	0.041 to 0.181
	SIESS	-0.082	0.034	-2.416	0.016	-0.149 to -0.016
	Time-lag	-0.059	0.040	-1.455	0.146	-0.138 to 0.020
Age	Intercept	0.211	0.070	3.017	0.003	0.074 to 0.349
	SIESS	0.012	0.023	0.542	0.588	-0.032 to 0.056
	Time-lag	-0.038	0.030	-1.245	0.213	-0.098 to 0.022

1548

1549 **Table S8.**

1550 Association between the relationship between putative sexual signal conspicuousness and

1551 attractiveness (Zr-attractiveness) and the relationship between putative sexual signal

1552 conspicuousness and other variables (benefits: Zr-benefits, individual condition: Zr-

1553 condition, body size: Zr-size, aggression or social dominance: Zr-dominance, traits related to

1554 sperm competition: Zr-sperm, and age: Zr-age), depending on two approaches (across- and

1555 within-studies) and two distinct models (uni- and bivariate). *N* indicates the number of effect

1556 sizes used in each approach. Shaded rows highlight estimates whose 95% confidence interval

1557 does not overlap zero.'

1558

Variable	Approach	*N*	Model	Estimate	95%CI
Benefits to sexual signal bearers or to their mates	Across-studies	66	Univariate	0.283	0.136 to 0.429
			Bivariate	0.739	0.359 to 0.985
	Within-studies	68	Univariate	0.246	0.102 to 0.390
			Bivariate	0.636	0.272 to 0.941
Individual condition	Across-studies	64	Univariate	0.218	0.053 to 0.383
			Bivariate	0.466	-0.078 to 0.922
	Within-studies	32	Univariate	0.330	0.085 to 0.574
			Bivariate	0.505	-0.056 to 0.944
Body size	Across-studies	59	Univariate	0.135	-0.077 to 0.347
			Bivariate	0.167	-0.309 to 0.639
	Within-studies	47	Univariate	0.003	-0.225 to 0.231
			Bivariate	-0.013	-0.663 to 0.667
Aggression or social dominance	Across-studies	24	Univariate	0.275	-0.102 to 0.653
			Bivariate	0.197	-0.551 to 0.796
	Within-studies	15	Univariate	0.199	-0.167 to 0.565
			Bivariate	0.057	-0.649 to 0.702
Traits related to sperm competition	Across-studies	13	Univariate	0.494	-0.126 to 1.114
			Bivariate	0.286	-0.820 to 0.970
	Within-studies	1	Univariate	-	-
			Bivariate	-	-
Age	Across-studies	39	Univariate	-0.076	-0.481 to 0.328
			Bivariate	0.001	-0.664 to 0.719
	Within-studies	30	Univariate	-0.086	-0.523 to 0.351
			Bivariate	0.118	-0.772 to 0.923

1559