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

Pietro Pollo[1,2]*, Malgorzata Lagisz[1,3], Renato Chaves Macedo-Rego[4], Ayumi Mizuno[1,3], Yefeng Yang[1], Shinichi Nakagawa[1,3]

[1] Evolution & Ecology Research Centre, School of Biological, Earth & Environmental Sciences, University of New South Wales, Kensington, NSW, 2052, Australia

[2] School of Environmental and Life Sciences, University of Newcastle, Newcastle, Australia

[3] Department of Biological Sciences, University of Alberta, CW 405, Biological Sciences Building, Edmonton, AB T6G 2E9, Canada

[4] Departamento de Biologia Geral, Universidade Federal de Viçosa, Av. Peter Henry Rolfs, Viçosa, Minas Gerais, 36570-000, Brazil

* Corresponding author: pietro_pollo@hotmail.com

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Abstract

Colourful body parts and bizarre displays that do not seem to contribute to the survival of individuals that express them have puzzled biologists for centuries. Sexual selection theory posits that these traits evolved because more conspicuous individuals attract more mates and experience greater fitness, yet evidence for this remains fragmented. Our augmented meta-meta-analysis of 41 meta-analyses, encompassing 375 animal species and 7,428 individual effect sizes, shows that the conspicuousness of (putative) sexual signals is positively related to mate attractiveness, fitness benefits, individual condition, and other characteristics (e.g. body size) of signal bearers. Most of these patterns are consistent across both taxa and sexes, underscoring the generalisability of our results. Furthermore, the strength of pre-copulatory sexual selection on conspicuousness is positively associated with the relationship between (i) conspicuousness and fitness benefits and (ii) conspicuousness and individual condition. This suggests that the relationships we assessed regarding trait conspicuousness would be stronger if we could select only traits that are truly used for mate attraction. Our study unifies several decades of knowledge on conspicuous traits, confirms many predictions made by the theory of sexual selection, and lays a clear path for the future of research on this topic.

Introduction

Extravagant body parts and elaborate displays 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 (Darwin 1871). If these traits are used as signals (i.e. for communication), they should be particularly conspicuous to their intended receivers (hereby *conspicuous traits*), such as conspecifics. This means that conspicuous traits might be unnoticeable to us if we do not have the sensory capacity to detect them (e.g. pheromones, electromagnetic fields). A common explanation for conspicuous traits is that more noticeable individuals can attract more or better mates, generating sexual selection for greater trait conspicuousness via mate choice (Andersson 1994; Darwin 1871; Rosenthal 2017). Consequently, conspicuous traits are often deemed "sexual ornaments" or "sexual signals", especially if they are sexually dimorphic (Pollo *et al.* 2024b).

Two challenges arise in the context of conspicuous traits and sexual signals. First, assessing how phenotypic variation influences signal effectiveness (i.e. trait conspicuousness) may be complex because (i) we do not know if the trait is indeed a signal; and (ii) if it is, which of its various aspects elicits responses from receivers (e.g. colour components [brightness, chroma, hue], size, symmetry, duration, intensity, other specific properties). For instance, considering individuals with vibrant colours as more conspicuous than drab ones assumes that higher chroma levels are more likely to trigger reactions from conspecifics (but possibly from predators as well). This means that labelling traits as conspicuous and assessing their conspicuousness rely on assumptions about which and how traits are used for communication, respectively. Second, a trait qualifies as a sexual signal (i.e. attractive to potential mates) only when its conspicuousness is positively associated with the mating success of its bearer (or associated proxies, e.g. pairing success, success in mate choice trials, social pair stability while other individuals divorce). As the strength of this relationship increases, so should the intensity of pre-copulatory sexual selection as mating success becomes concentrated among individuals with highly conspicuous traits. Unfortunately, researchers may presume that the conspicuous traits they examine are used for mate attraction without evidence (e.g. Gil & Slater 2000; Greenspan *et al.* 2016; Quinard *et al.* 2017), making these traits *putative* sexual signals, potentially mixing actual sexual signals with other non-sexually selected traits and thus possibly drawing misleading conclusions on the evolution of conspicuous traits.

Despite the challenges associated with them, sexual signals became popular within the sexual selection literature since the 1970s, culminating in the development of many theoretical models attempting to explain their evolution through mate choice (reviewed in Kokko *et al.* 2003 and Kuijper *et al*. 2012). These models usually predict that sexual signal conspicuousness increases the fitness of their bearers (e.g. by making them more attractive) but also 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”)(Andersson 1994; Kokko *et al.* 2003; Lindsay *et al.* 2019). The theory also predicts that sexual signal conspicuousness is condition-dependent, so sexual signals act as honest indicators of individual condition (Rowe & Hole 1996). According to the genic capture hypothesis, sexual selection on these traits does not erode genetic variation because of the many genes determining condition (Rowe & Hole 1996). Moreover, sexual signal conspicuousness may covary with the expression of other traits that can also be under selection (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 Pollo *et al.* 2024b). However, to be feasible, studies (including meta-analytical ones) focus on one or few fitness-related variables (e.g. parasite load: Dougherty *et al.* 2023; survival: Romano *et al.* 2017b), types of conspicuous traits (e.g. colourful plumage: Guindre-Parker & Love 2014; Hegyi *et al.* 2015; song traits: Garamszegi 2005; Garamszegi & Møller 2004), taxa (e.g. birds: Nakagawa *et al.* 2007; Romano *et al.* 2017a, b; Yasukawa *et al.* 2010), and sex (e.g. males: Gontard-Danek & Møller 1999; Koch *et al.* 2016; McLean *et al.* 2012). The last one is particularly emblematic because most of the theory regarding sexual signals has been developed considering only males as their bearers, even though females possess conspicuous traits in many species (Amundsen 2000) and males can express mate choice (Bonduriansky 2001; Edward & Chapman 2011; Pollo *et al.* 2022). Because of limitations in the scope of individual meta-analyses, valuable knowledge of conspicuous traits assumed to be sexual signals remains scattered across the literature, which precludes us from holistically understanding these traits. For example, we currently lack insight on whether the relationship between conspicuous traits and fitness-related variables generally depends on the sex of individuals expressing these traits or on trait modality.

Here, we compiled and analysed 7,428 effect sizes from 1,196 empirical studies (used as data sources by 41 meta-analyses) to investigate the relationship between the conspicuousness of putative sexual signals and their bearers' attractiveness, fitness, individual condition, and other traits (Table S1; Fig. 1), predicting that all these relationships are positive. Our dataset encompasses data from 375 animal species in total (Fig. 2). Note that part (but not all) of the data we used in our study were directly extracted from empirical studies and a substantial proportion of these data were not analysed by any of the 41 meta-analyses mentioned (see also Pollo *et al.* 2025). In other words, we conducted a second-order meta-analysis (i.e. meta-meta-analysis) augmented with additional data. Moreover, we used a tailored approach for each trait and species in our dataset using information provided by our data sources (i.e. empirical studies and meta-analyses) to determine what trait conspicuousness entailed (see Table S2).

We verified the role of two moderators in the relationships assessed in our study. First, considering that sexual selection is typically proposed to act more strongly on males than on females (Bateman 1948; Darwin 1871; Janicke *et al.* 2016), we assessed the effect of the sex of signal bearers (male *vs.* female) on the relationships between the conspicuousness of putative sexual signals and the variables within our framework. Second, in comparison with colour and morphology (hereby *fixed traits*), behavioural signals (hereby *flexible traits*, available only for males in our dataset) can profusely vary in short periods and thus are more likely to reflect their bearers' current condition (Dougherty 2021). Although this means that trait type (flexible *vs.* fixed) should primarily affect the relationship between putative sexual signal conspicuousness and individual condition, we tested the role of trait type in all the relationships we assessed. Additionally, we verified an implicit assumption commonly made by biologists that, to our knowledge, has never been tested: that the strength of pre-copulatory sexual selection (from attracting mates but not from intrasexual competition) on the conspicuousness of a trait is linked to the strength of the relationship between the conspicuousness of that trait and the benefits it signals. The predicted positive association between these two relationships (i.e. conspicuousness-attractiveness and conspicuousness-benefits) stems from models suggesting that mating preferences intensify with increasing variation in mate quality (Johnstone *et al.* 1996; Parker 1983). Furthermore, such an association is central to understanding sexual selection because a relationship between conspicuousness and fitness (e.g. reproductive success) can arise from both natural and sexual selection (Anthes *et al*. 2017; Henshaw *et al*. 2018). Despite not having further theoretical expectations, we extended this rationale by verifying whether the strength of pre-copulatory sexual selection on the conspicuousness of a trait is linked to the strength of the relationship between the conspicuousness of that trait and the condition and other traits of its bearer.

Material and Methods

General

Our methodology was described in our pre-registration (Pollo *et al.* 2024a) and in a twin study that essentially used the same dataset as we did in the present study (Pollo *et al.* 2025). Deviations from our pre-registration are shown in Appendix 1. Author contributions are reported using MeRIT guidelines (Nakagawa *et al.* 2023) and the CRediT statement (McNutt *et al.* 2018).

Terminology: putative sexual signals, conspicuousness, and variables within our framework

Our dataset contains information on the relationship between putative sexual signal conspicuousness and many other variables (Table S1; Fig. 1). Putative sexual signals refer to traits thought to be involved in mate attraction (by authors of empirical papers or of primary meta-analyses that were used as data sources; weapons or body size were not considered valid putative sexual signals; see also McCullough *et al.* 2016). On the other hand, trait conspicuousness refers to the hypothesised relationship between phenotypic variation and response from signal receivers. Then, in the context of sexual signals (i.e. putative sexual signal conspicuousness), the hypothesised relationship between trait expression and attractiveness to mates. 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. sounds with higher frequency are expected to be more appealing for birds (Garamszegi 2005) but less appealing for amphibians (McLean *et al.* 2012). PP ascertained the expected direction of attractiveness (i.e. putative sexual signal conspicuousness) based on information provided by authors of empirical and primary meta-analyses (see Table S2) but note that what is considered more appealing to mates according to these authors has often not been tested. In fact, PP was unable to infer the expected direction of attractiveness for certain traits when he directly extracted data from empirical studies. Effect sizes with ambiguous direction also occurred because of unclear reporting of results (e.g. p-values provided without direction). In total, 6.2% of all our effect sizes (464 out of 7,428) were ambiguous in direction. PP then made additional analyses (see below) in which effect sizes with ambiguous direction were removed or changed to their opposite value to ensure our results were robust (see Table S3).

Variables within our framework (Fig. 1) are explained throughout the manuscript as results are reported, while their direction and more examples are given in Table S1. Yet, we clarify two specific complex concepts here. First, “benefits” refer to fitness-related proxies of conspicuous trait bearers as well as to fitness gains shared with or originating from bearers’ mates. This is because these benefits stem from traits and decisions of both pairing individuals (e.g. mating date and number of eggs laid). Second, we classify stress-related circumstances as “external conditions”, which can be a product of natural variation (e.g. with quality of habitat or parental care received earlier in life) or of experimental manipulation (e.g. modifying diet quality or quantity, or even the number of eggs in the nest, which induce distinct reproductive effort in the form of parental care). Note that meta-analyses’ authors were often vague regarding the exact data they extracted, so interconnected proxies, such as reproductive success and viability measures, were difficult to separate. For instance, whether "fledgling success" means number of fledglings (reproductive success) or proportion of offspring that fledged from all eggs laid (viability) was unclear in many cases, so PP deemed most of them as reproductive success given that this is a more diverse measure.

Selection of meta-analyses

A recent systematic map of meta-analyses on topics related to sexual selection (Pollo *et al.* 2024b) identified 152 meta-analyses focusing on questions associated with sexual selection. In November 2023, PP first selected 60 of these meta-analyses based on the questions they asked, which were summarised by Pollo *et al.* 2024b. PP specifically identified meta-analyses that asked questions involving pre-copulatory sexual traits (59 meta-analyses had already been identified this way by Pollo *et al.* 2024b, only Møller & Thornhill 1998 was not; see Supplementary file). However, only 44 of these 60 meta-analytical studies were eligible for inclusion in our meta-meta-analysis because the remaining 16 did not examine the relationship between putative sexual signals and variables within our framework (Fig. 1; Table S1; see section above). PP then included an additional meta-analysis, which examined the relationship between sexual ornaments and parasite load (Dougherty *et al.* 2023), that was published after the initial search in Pollo *et al.* (2024b). A total of 45 meta-analyses were thus eligible for inclusion in the present study, but data could not be retrieved for four of these meta-analyses (see details in Pollo *et al.* 2025). Therefore, 41 meta-analyses were included in our study (Dougherty 2021; Dougherty *et al.* 2023; Evans *et al.* 2010; Fiske *et al.* 1998; Garamszegi 2005; Garamszegi *et al.* 2007; Garamszegi & Eens 2004; Garamszegi & Møller 2004; Gontard-Danek & Møller 1999; Griffith *et al.* 2006; Guindre-Parker & Love 2014; Hegyi *et al.* 2015; Hernández *et al.* 2021; Jennions *et al.* 2001; Koch *et al.* 2016; Mautz *et al.* 2013; McLean *et al.* 2012; Meunier *et al.* 2011; Møller & Alatalo 1999; Møller & Jennions

2001; Møller & Thornhill 1998; Moore *et al.* 2016; Nakagawa *et al.* 2007; Nolazco *et al.* 2022; Parker 2013; Parker *et al.* 2006; Parker & Ligon 2003; Prokop *et al.* 2012; Robinson & Creanza 2019; Romano *et al.* 2017a, b; Sánchez-Tójar *et al.* 2018; Santos *et al.* 2011; Simons *et al.* 2012; Simons & Verhulst 2011; Soma & Garamszegi 2011; Street *et al.* 2016; Thornhill & Møller 1998; Weaver *et al.* 2018; White 2020; Yasukawa *et al.* 2010).

Data collection

Our data collection is fully reported in Pollo *et al.* (2025). Briefly, PP compiled individual effect sizes from the 41 primary meta-analyses included in our study (see above), which contained relevant data for our study from 1,196 unique empirical sources (i.e. after deduplication). Then, all authors (re-)extracted all data related to putative sexual signals from 243 empirical studies that these meta-analyses used as sources (see *Appendix 2*). Most of these studies were selected because multiple meta-analyses used them and produced mismatching individual effect sizes (Pollo *et al.* 2025). This process was done as part of a reproducibility and replicability project (Pollo *et al.* 2025) but also provided the base to the present study as it essentially deduplicated and ensured the quality of our dataset (see below). After data re-extractions, PP replaced the individual effect sizes reported by meta-analyses with re-extracted effect sizes for these 243 empirical studies. Other effect sizes reported by meta-analyses (from empirical studies whose data we did not re-extract) were maintained in the dataset. Despite these 243 empirical studies being cited as data sources by meta-analyses, many of the effect sizes re-extracted by us were not actually reported by primary meta-analyses or, alternatively, were reported by primary meta-analyses with a different value from the ones we obtained during re-extraction (see Pollo *et al.* 2025). Thus, to some extent, our dataset contains data that have not been used in previous meta-analyses. PP additionally removed identically reported effect sizes (both in description and in value) from other duplicated empirical studies (those that we did not extract data from). This process ensured that all individual effect sizes in our dataset were unique, in contrast to meta-meta-analyses that analyse mean effect sizes from primary meta-analyses (e.g. Castellanos & Verdú 2012; Hillebrand *et al.* 2020; Tamburini *et al.* 2020), which can encompass repeated data (as the same empirical studies can be used by multiple primary meta-analyses). PP further removed from the dataset data related to parental care provided after manipulation of putative sexual signals (e.g. Johnsen *et al.* 2005), as this was not considered a proper test of the relationship attractiveness-parental care. After these procedures, our dataset tallied 7,428 effect sizes, with 4,237 of them (57% of the dataset) being extracted by us and the remaining effect sizes being originally reported by primary meta-analyses. PP used Fisher's Zr as an effect size, transforming it to correlation coefficient (r) when reporting most of the results. Details on the calculation of effect sizes, including all equations used, are reported in Pollo *et al.* (2025).

Analyses

PP constructed separate meta-analytical models to verify the relationship between putative sexual signal conspicuousness and each variable within our framework, resulting in seven sets of models (one set for each background colour in Figs. 3 and 4). PP used multilevel meta-analytical models because effect sizes were not independent of one another. Different effect sizes could share the same (empirical) study ID, species ID, and trait type ID (i.e. flexible or fixed trait nested within-species). Thus, in addition to effect size ID, PP used these variables as random factors in our models to control for non-independence. PP also included a correlation matrix related to phylogenetic relatedness for the species in our model as a random factor (Nakagawa & Santos 2012). From meta-analytical models with all these random factors, PP quantified I^2_{total} (a measure of heterogeneity not attributed to sampling error; Higgins *et al.* 2003) and how much of it each random factor explained (partial I^2; see

Table S4). PP fitted meta-analytical models with the following fixed factors: none (only intercept, showing the average relationship), sub variable (only models involving benefits and individual condition, see Table S1), sex (male, female, or unknown) and trait type (fixed or flexible), all together. PP followed Cohen (1988) to interpret the magnitude to mean effect sizes (as *Zr*, before converting them to *r*, “weak” for values up to 0.2, “moderate” for values up to 0.5, and “high” for greater values).

PP also constructed additional versions of all models described above, in which he removed or inverted the signal of data points whose direction was ambiguous (e.g. putative sexual signals without information on expected direction for mate attraction or data with direction not clearly reported in empirical studies). The results of these analyses were very similar to the ones with data points as originally extracted (Table S3).

PP tested for signs of publication bias in meta-analytical models using three approaches (see Table S7, Figs. S1 and S2). First, PP visually evaluated funnel asymmetry for each model using funnel plots, which show the residuals of meta-analytical models containing all moderators against effect sizes’ precision (i.e. inverse of standard error). Second, PP further assessed funnel asymmetry with an alternative approach to Egger’s regression: using the inverse of the effective sample size as a moderator in a multilevel meta-analytical model (Nakagawa *et al.* 2021a). Third, in the same meta-analytical models of the second approach, PP verified time-lag bias using publication year as a moderator (Jennions & Møller 2002).

To verify whether the relationship between putative sexual signal conspicuousness and attractiveness is associated with the relationship between putative sexual signal conspicuousness and other variables within our framework, PP sought conspicuous traits in our dataset with both of these relationships. PP used two approaches to collect and link these data. In the first approach (hereby *across-studies*, Fig. 5), PP calculated a mean effect size for each putative sexual signal (across different empirical studies examining a given species) regarding the relationship between its conspicuousness and attractiveness to mates (Zr-attractiveness). PP then linked these estimates to mean effect sizes regarding the relationship between the conspicuousness of that same putative sexual signal and another variable (Zr-benefits, Zr-condition, etc.), also across different empirical studies examining a given species. This first approach assumes that the relationship between attractiveness and putative sexual conspicuousness across time and populations is consistent, which is not necessarily true (Chaine & Lyon 2008). To ameliorate this issue, our second approach (hereby *within-studies*; Fig. S3) only links these relationships (Zr-attractiveness with either Zr-benefits, Zr-condition, Zr-size, Zr-dominance, Zr-sperm, or Zr-age) extracted from the same empirical study. This second approach is more reliable but yields fewer data points, such that the relationship between Zr-attractiveness and Zr-sperm could not be analysed with this second approach as a single data point was available. We only show the results of the first approach in the manuscript as both approaches generated similar qualitative results.

Meta-regressions described above accounted for the variation of effect sizes serving as the response variables (i.e. Zr-benefits, Zr-condition, etc.) but disregarded the dispersion of effect sizes serving as predictor variables (i.e. Zr-attractiveness). In other words, they are univariate models. To correct this, PP conducted bivariate models, in which the dispersion of both response and predictor variables is considered. However, this approach yields much larger confidence intervals and estimates generated may not be reliable as we could not preclude divergent transitions in MCMC chains when running these analyses, which may indicate that posterior distributions are unreliable. Thus, we preferred to show results of only univariate models (with the across-studies approach) in the manuscript, but results for other approaches and models can be found in Table S8.

All statistical analyses were conducted in the software R 4.4.0 (R Core Team 2024). PP fitted meta-analytical models (except for bivariate models) using the *rma.mv* function from the package *metafor* 4.6.0 (Viechtbauer 2010). Bivariate models were fitted using the package *brms* 2.22.0 (Bürkner 2017), in which PP ran three chains, each with 10,000 iterations plus another 10,000 burn-in iterations. In these analyses, PP adopted Stan's standard uninformative priors and set the maximum tree depth to 12 and the adaptive delta to 0.999. PP calculated R^2 (Nakagawa & Schielzeth 2013), I^2, CV, and M^2 (Yang et al. 2024) using, respectively, the *r2_ml*, *i2_ml*, *cvh2_ml*, and *m2_ml* function from the package *orchaRd* 2.0 (Nakagawa *et al.* 2021b). Phylogenetic trees were built using the packages *ape* 5.8 (Paradis & Schliep 2019) and *rotl* 3.1.0 (Michonneau *et al.* 2016). PP performed pairwise comparisons (two-tailed z-tests) using the function *glht* from the package *multcomp* 1.4.26 (Hothorn *et al.* 2008).

Results

Attractiveness to prospective mates

We found that putative sexual signal conspicuousness is, on average, (moderately) positively related to attractiveness to individuals of the opposite sex ($r = 0.329$, 95%CI = 0.233 to 0.419; Table S3; Fig. 3). This result is consistent across species given the low heterogeneity at the level of species ($I^2_{[\text{species = species ID + phylogeny}]} = 2.3\%$) and therefore potentially generalisable, despite the high overall heterogeneity across effect sizes ($I^2_{\text{total}} = 91.5\%$; Table S4).

Benefits to signal bearers and to their mates

We found that putative sexual signal conspicuousness is, on average, (weakly) positively related to benefits to their bearers and to their mates ($r = 0.165$, 95%CI = 0.133 to 0.197;

Table S3; Fig. 3). However, we detected evidence of publication bias for these data, so the actual relationship might be even weaker as positive effect sizes were overrepresented (Fig. S1D-F, Table S7). This finding is potentially consistent across species ($I^2_{\text{[species = species ID + phylogeny]}}$ = 0.7%; Table S4). Furthermore, we found that males show, on average, a stronger relationship between putative sexual signal conspicuousness and benefits compared with females (Table S5). We note that these results come from an amalgamation of metrics (Fig. 1), so we discuss each of them in detail below.

First, more conspicuous putative sexual signals are, on average, (moderately) associated with earlier arrival at breeding sites, earlier pairing, or earlier reproduction (hereby simply *earlier timing*; r = 0.213, 95%CI = 0.171 to 0.254; Table S3; Fig. 3), a relationship that is stronger in males than in females (Table S5). Second, putative sexual signal conspicuousness is, on average, (weakly) positively related to reproductive success (e.g. number of offspring; r = 0.157, 95%CI = 0.121 to 0.193; Table S3; Fig. 3). We also note that the conspicuousness of male flexible putative sexual signals is more strongly associated with reproductive success than that of male and female fixed putative sexual signals (Table S5). Third, putative sexual signal conspicuousness is, on average, (weakly) positively related to offspring viability (e.g. proportion of eggs hatched) or quality (e.g. offspring size, see also Table S1) (r = 0.164, 95%CI = 0.123 to 0.205; Table S3; Fig. 3). 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). 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). 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).

Individual condition

We found that putative sexual signal conspicuousness is, on average, (weakly) positively related to distinct measures of individual condition (r = 0.174, 95%CI = 0.124 to 0.224; Table S3; Fig. 4). Yet, this result can be overestimated as we found evidence of publication bias for these data (Fig. S1G-I; Table S7). This result is potentially generalisable across taxa ($I^2_{[\text{species = species ID + phylogeny}]}$ = 6.1%; Table S4). Moreover, we found that males show, on average, a stronger relationship between fixed putative sexual signal conspicuousness and individual condition compared with females (Table S5).

Individual condition can be measured in many ways (Fig. 1), so we also verified the relationship between each individual condition proxy and putative sexual signal conspicuousness separately. First, putative sexual signal conspicuousness is, on average, (moderately) positively associated with beneficial (external) conditions (e.g. better diet, lower reproductive effort, etc.; r = 0.263, 95%CI = 0.215 to 0.31; Table S3; Fig. 4). Second, putative sexual signal conspicuousness is, on average, (weakly) positively associated with body condition (e.g. body mass controlled for structural body size; Jakob *et al.* 1996; r = 0.198, 95%CI = 0.161 to 0.235; Table S3; Fig. 4). Yet, conspicuousness of fixed putative sexual signals is, on average, more strongly associated with body condition in males than in females (Table S5). Third, putative sexual signal conspicuousness is, on average, (weakly) positively associated with immune or antioxidant capacity (r = 0.129, 95%CI = 0.084 to 0.174; Table S3; Fig. 4). Fourth, putative sexual signal conspicuousness is, on average, (weakly) positively associated with parasite resistance (i.e. opposite of parasite load; r = 0.119, 95%CI = 0.078 to 0.159; Table S3; Fig. 4). Fifth, putative sexual signal conspicuousness is, on average, (weakly) positively associated with survival (r = 0.113, 95%CI = 0.053 to 0.172; Table S3; Fig. 4). However, the relationship between putative sexual signal conspicuousness and survival was greater for males than for females, with the latter being essentially zero (Table S3; Table S5; Fig. 4).

Other traits

We found that putative sexual signal conspicuousness is, on average, (moderately) positively related to body size (r = 0.23, 95%CI = 0.144 to 0.312; Table S3; Fig. 4), an apparently generalisable finding across species ($I^2_{[\text{species = species ID + phylogeny}]}$ = 3.6%; Table S4). We also found that putative sexual signal conspicuousness is, on average, (moderately) positively related to aggression and social dominance (e.g. greater number of aggressive behaviours performed to hetero- and conspecific intruders; r = 0.205, 95%CI = 0.047 to 0.354; Table S3; Fig. 4). However, this result is not as generalisable across species as our other findings ($I^2_{[\text{species = species ID + phylogeny}]}$ = 14.6%; Table S4). Furthermore, we found that putative sexual signal conspicuousness is, on average, (weakly) positively related to the expression of traits that increase success in sperm competition (e.g. more or better sperm, larger testes; r = 0.107, 95%CI = 0.029 to 0.185; Table S3; Fig. 4). This result appears to be generalisable across taxa, but not across studies ($I^2_{[\text{species = species ID + phylogeny}]}$ = 1.2%, $I^2_{\text{across-studies}}$ = 43%; Table S4). Interestingly, we also detected that flexible putative sexual signals were more strongly related to the expression of sperm competition-related traits than fixed putative sexual signals (Table S5). Lastly, we found that putative sexual signal conspicuousness is, on average, (weakly) positively related to age (r = 0.196, 95%CI = 0.043 to 0.34; Table S3; Fig. 4), a result that may be generalisable across species ($I^2_{[\text{species = species ID + phylogeny}]}$ = 7.4%; Table S4).

Strength of pre-copulatory sexual selection on relationships between conspicuousness and other variables

We found that the attractiveness-conspicuousness relationship (i.e. Zr-attractiveness), which can be taken as a coarse proxy of pre-sexual selection stemming from mate choice on putative sexual signal conspicuousness, is positively associated with the relationship between putative sexual signal conspicuousness and both the benefits they provide (Fig. 5A; Fig. S3A) and bearers' individual condition (Fig. 5B; Fig. S3B; Table S8). However, we found no evidence that pre-copulatory sexual selection on putative sexual signal conspicuousness is associated with the relationship between putative sexual signal conspicuousness and other traits (Fig. 5C-F; Fig. S3C-E; Table S8). Nonetheless, data for these analyses were scarce (Table S8), so these results require extra caution as they might not be generalisable.

Discussion

Attractiveness to prospective mates

We found that the conspicuousness of putative sexual signals is, on average, (moderately) positively related to attractiveness to prospective mates, a result that is consistent across taxa. However, the high overall heterogeneity across effect sizes we found exposes a huge variability in this relationship. This means that not all traits (or at least not all their components) deemed potentially attractive to mates are, in fact, sexual signals. This is especially relevant for the other relationships we assess in our manuscript because it emphasises that some of the traits in our dataset do not play a role in sexual selection despite being conspicuous (to us and/or to conspecifics).

Benefits to signal bearers and to their mates

We found that putative sexual signal conspicuousness is, on average, (weakly) positively related to benefits to their bearers and to their mates. Unfortunately, we cannot differentiate direct from indirect benefits, as this requires a more complex approach than the one we provide here (see meta-analyses exploring this in-depth, e.g. Prokop *et al.* 2012; Prokuda & Roff 2014).

Regarding our results on specific benefit proxies, we first found that putative sexual signal conspicuousness is, on average, (moderately) associated with earlier timing (to arrive at breeding site, to pair, to mate, to breed, to hatch eggs, or to fledge offspring; Table S1). This measurement can represent individual quality and attractiveness, and may lead to more reproductive opportunities and a better environment for the offspring (Price *et al.* 1988).

We also found that putative sexual signal conspicuousness is, on average, (weakly) positively related to reproductive success. Various mechanisms can produce this relationship. For instance, given that individuals with traits that are more conspicuous tend to be more attractive, these individuals should experience greater mating success and consequently increase their reproductive success if mating with multiple individuals is advantageous (i.e. when Bateman's gradient is positive, generally assumed for males but rarely for females; Bateman 1948). Moreover, individuals with more conspicuous sexual signals might be more likely to select mates that can provide them with more benefits (Pollo *et al.* 2022), increasing their own fitness. Individuals with more conspicuous sexual signals may also receive greater reproductive investment from their partners than their counterparts (Horváthová *et al.* 2011). A positive relationship between sexual signal conspicuousness and reproductive success can arise from a positive association between putative sexual signal conspicuousness and (female) fecundity (e.g. Lüdtke & Foerster 2019; Mobley *et al.* 2018) or reproductive investment beyond just gametes (e.g. parental care, see below), which would make these conspicuous traits signals of direct benefits to mates. Here, we cannot determine which of these mechanisms more frequently explains why individuals with more conspicuous putative sexual signals show greater reproductive success. Future studies should then address this gap by disentangling the various effects on reproductive success, e.g. controlling for the number of matings that attractive and unattractive individuals obtain and standardising parental care provided to the offspring.

In addition, we found that putative sexual signal conspicuousness is, on average, (weakly) positively related to offspring viability or quality. This represents that more conspicuous sexual signals may indicate that their bearers possess “good genes” that can be passed to the offspring, possibly increasing offspring’s viability and quality (Andersson 1994). However, the same arguments made for reproductive success (e.g. greater reproductive effort from partners) also apply to offspring’s viability or quality because they result from genes and investment in the offspring from both parents.

Our finding that putative sexual signal conspicuousness is, on average, (weakly) positively related to paternity success 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). Yet, 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 (Macartney *et al.* 2024).

Furthermore, our finding that putative sexual signal conspicuousness is, on average, (weakly) positively related to the amount of parental care expressed by the signal bearer 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 (Hegyi *et al.* 2015).

Lastly, we found that putative sexual signal conspicuousness is, on average, (moderately) positively related to territory quality. 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. Butchart *et al.* 1999).

Individual condition

We found that putative sexual signal conspicuousness is, on average, (weakly) condition-dependent. Importantly, this relationship was detected when examining proxies of individual condition separately, and was even stronger when the proxy in question was an external condition. Two hypotheses in the literature explain how condition-dependent sexual signals represent honesty: the costly signalling principle (first proposed by Zahavi 1975) and the index hypothesis (e.g. Hamilton & Zuk 1982). The former states that the expression and maintenance of sexual signals require resources that could be spent elsewhere (Zahavi 1975), with higher-quality individuals being expected to deal more effectively with metabolic trade-offs and thus being able to be more ornamented (Getty 2006; Grafen 1990). On the other hand, the index hypothesis does not invoke resource trade-offs to explain sexual signals' condition-dependence, but rather posits that these traits evolve as honest signals of condition by sharing pathways with basic physiological processes (Hill 2011; Hill *et al.* 2023; Maynard Smith & Harper 1995). These hypotheses are contentious as each has different underlying concepts, with multiple authors proposing distinct features and predictions (see Weaver *et al.* 2017). Even though our results support the ultimate pattern predicted by these two hypotheses (i.e. sexual signal conspicuousness is condition-dependent), we cannot elucidate which of them is more likely to explain this pattern.

Other traits

We found that putative sexual signal conspicuousness is, on average, positively related to various other traits: moderately so for body size and social dominance, and weakly so for traits related to sperm competition and age.

Body size can be under positive directional selection if larger individuals are more fecund (Honěk 1993) or experience greater success in intrasexual competition (Andersson 1994). Given that sexual signal conspicuousness is also predicted to be under positive directional sexual selection (Kokko *et al.* 2006), a positive relationship between sexual signal conspicuousness and body size can occur. In such a scenario, trait conspicuousness would signal direct benefits to prospective mates. However, larger body size can be constrained or even disfavoured in some taxa (e.g. Székely *et al.* 2004), so this rationale is not universal.

Greater trait conspicuousness may also signal one's status to others interested in battling for resources, ultimately deterring costly fights (Rohwer 1975). Note that, *a priori*, if these resources are not mates, these signals have no connection to pre-copulatory sexual selection stemming from mate choice, highlighting that conspicuous traits might not necessarily be sexual signals. Yet, conspicuous traits that signal to rivals can also be used for mate selection, even if this is not their primary function. After all, greater success in competition for resources should be related to greater access to resources, meaning possible benefits to mates (e.g. territory quality, more competitive offspring if heritable).

Highly ornamented males could be wasting resources by investing in traits related to sperm competition if, being more attractive, they can experience a lower risk of sperm competition by biassing cryptic female choice in their favour (e.g. Pilastro *et al.* 2004) or reducing the chances that females they mate with remate with another male (e.g. Kiyose *et al.* 2022). However, traits that enhance sperm competition success are potentially under positive directional selection for all males (Mautz *et al.* 2013; but see Dougherty *et al.* 2022) and thus may be expected to covary with sexual signal conspicuousness. Alternatively, this pattern can occur if male ornamentation honestly signals their fertilisation ability to females (Mautz *et al.* 2013).

Sexual signal conspicuousness should increase with age (but see Dougherty 2021) as older individuals are under greater terminal investment selection (i.e. to increase reproductive effort before dying; Clutton-Brock 1984; Foo *et al.* 2023). Moreover, when sexual signal conspicuousness is positively related to age, trait conspicuousness essentially signals individual ability to survive for longer (Kokko 1998). We note, however, that our results regarding age might be conflated by mating experience (i.e. older individuals are more likely to have mated than their younger counterparts), although a meta-analysis controlling for this showed a similar result (Dougherty 2021).

Sex and trait type interactions

We found that, compared with male fixed putative sexual signals, the conspicuousness of female fixed putative sexual signals is, on average, less condition-dependent and more weakly related to the benefits provided to bearers and to mates. However, these sex differences only emerged when analysing all proxies of these variables together, or when evaluating some specific proxies separately, such as timing, body condition, and survival. Therefore, our results only partially support the predictions that originate from the idea that males are under stronger sexual selection than females (Bateman 1948; Darwin 1871; Janicke *et al.* 2016). Most importantly, our findings indicate that the conspicuousness of putative sexual signals in both males and females are, on average, associated with greater benefits to bearers and to mates, greater individual condition, and body size. This emphasises that researchers need to consider the role of individuals of both sexes when exploring processes and patterns related to sexual selection.

Contrasting with the sex differences we found, our results show that trait type rarely played a role in the relationships between various factors and the conspicuousness of putative sexual signals. More specifically, considering only male putative sexual signals, the conspicuousness of flexible traits was more strongly related to signal bearers' reproductive success and ability in sperm competition than fixed traits. These findings might be affected by limited or absent data on behavioural signals (i.e. displays) in our dataset for males and females, respectively.

Strength of pre-copulatory sexual selection on relationships between conspicuousness and other variables

The relationships between conspicuous traits and multiple variables we explored in previous sections involved traits *assumed* to be preferred by mates (i.e. putative sexual signals). Still, these traits could actually be unattractive to mates or attractive in the opposite direction than the one predicted (e.g. preference for dull colours instead of vivid colours). We thus assessed whether the conspicuousness of traits more strongly related to attractiveness to prospective mates were also more strongly related to benefits to signal bearers and their mates, individual condition, and other traits. We found evidence supporting this for benefits and individual condition, but not for other traits.

Theory predicts that mate choosiness, and thus pre-copulatory sexual selection stemming from mate choice, increases with variation in mate quality (Johnstone *et al.* 1996; Parker 1983). Therefore, the positive relationship we found between Zr-attractiveness and Zr-benefits is expected, but what about other variables? Although we are unaware of theoretical studies predicting that greater sexual selection on conspicuousness intensifies its condition-dependence (generating the positive relationship between Zr-attractiveness and Zr-condition we found), this might be plausible as an escalation of honest signalling. By contrast, the relationship between conspicuousness and other traits might be more variable because greater body size, social dominance, expression of traits related to sperm competition, and age may lead to benefits to their bearers only in certain situations. Perhaps the most valuable insight from these results is that even when Zr-attractiveness is zero (i.e. no link between attractiveness and conspicuousness) or negative (i.e. attractiveness decreases with conspicuousness), other relationships between conspicuousness and distinct variables (e.g. Zr-benefits, Zr-condition) can be positive (and vice-versa). This means that researchers should not assume that positive relationships between putative sexual signal conspicuousness and different variables attest that they are, indeed, sexually selected.

Limitations and future opportunities

Given that the relationship between the conspicuousness of putative sexual signals and attractiveness to mates represents the core of the theory on mate choice, and that our dataset represents the information collected by most meta-analyses on putative sexual signals, it is astonishing that this relationship was available for only a quarter of the species (Fig. 2) and represented less than 8% of all effect sizes in our dataset. However, our data regarding the attractiveness of conspicuous traits derived from empirical studies retrieved by only 15 meta-analyses (out of 41 we included in our study), with 11 of them focusing exclusively on one or multiple species of birds. Thus, it is possible that more data on the attractiveness of conspicuous traits could be available from the primary literature, especially for non-avian species. Yet, the conspicuousness-attractiveness relationship was available for only 32.5% of the bird species in our entire dataset (62 out of 191), revealing that meta-analyses are not properly exploring this relationship even for well-studied taxa or, more likely, that such data do not exist in the primary literature. Therefore, it might be fair to infer that biologists often inspect associations between conspicuous traits and their potential benefits or costs without attesting to the attractive function of these traits in the first place. However, we remind researchers that conspicuous traits can serve purposes other than mate attraction, such as to signal status to conspecifics regardless of sex (see previous sections), to deter (Mizuno *et al.* 2024) or confuse (Franklin *et al.* 2024; Henríquez-Piskulich *et al.* 2023) predators, or to avoid sexual harassment (Falk *et al.* 2021). Therefore, it is imperative to first examine the primary function of conspicuous traits, as making assumptions about them can hamper our knowledge about their evolution. In fact, our findings that signals under stronger mate choice are more strongly associated with benefits they provide and with their condition-dependence suggest that the relationships we assessed throughout our study (i.e. between putative sexual signals and benefits, condition, and traits) should be much stronger if we could identify and select only the signals that are truly attractive to mates.

In addition to the paucity of information related to the attractiveness of conspicuous traits, our dataset may amplify limitations and biases from primary meta-analyses that we used as sources. For example, we found signs of publication bias, which may affect the magnitude of our estimates. Furthermore, half of the species in our dataset are birds (Fig. 2) as most meta-analyses that we collected data from focus on bird colouration, resulting in a dataset where other traits and animal groups (e.g. invertebrates) are underrepresented (Figs. S4 and S5). Notably, female behaviours as putative sexual signals were almost absent from our dataset despite being ubiquitous in nature (e.g. pheromones; Wyatt 2014) and potentially subjected to sexual selection (Johansson & Jones 2007), possibly leading to similar patterns to the ones we found for other putative sexual signals (e.g. condition-dependence; Harari *et al.* 2011). Although more data may have become available after the primary meta-analyses we used as data sources were published (i.e. data not included in our dataset), information on female behavioural sexual signals and other neglected topics likely remains scarce. Collecting data on overlooked traits and taxa should address these gaps and may even challenge our perceptions, such as of stereotypical sex roles (Ah-King 2022a, b; Pollo & Kasumovic 2022). However, stronger incentives may be necessary to achieve this goal (Pollo *et al.* 2024b).

While our study represents a solid advancement for the theory of sexual selection by testing many of its predictions, and most of our results appear generalisable across taxa, we stress that conspicuous traits in nature are extremely diverse. This means that existing and future primary studies and meta-analyses on sexual signals remain valuable if they provide in-depth investigations on factors that are unique to certain conspicuous traits (e.g. type of pigment for colourful traits; Weaver *et al.* 2018). More importantly, the diversity we see in nature reinforces the urgency in acquiring data beyond certain conspicuous traits and taxonomic groups. Failing to do so risks leaving us with biassed and stagnant evidence, dimming the spark that Darwin ignited over 150 years ago.

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Author contributions

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

Data curation: PP

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

Methodology: PP, SN

Project administration: PP

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Supervision: SN

Visualisation: PP

Writing – original draft: PP, SN

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

Competing interests

We declare no competing interests.

Data and code availability

All data and code used in this study are available at: https://osf.io/6njem/.

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Figures

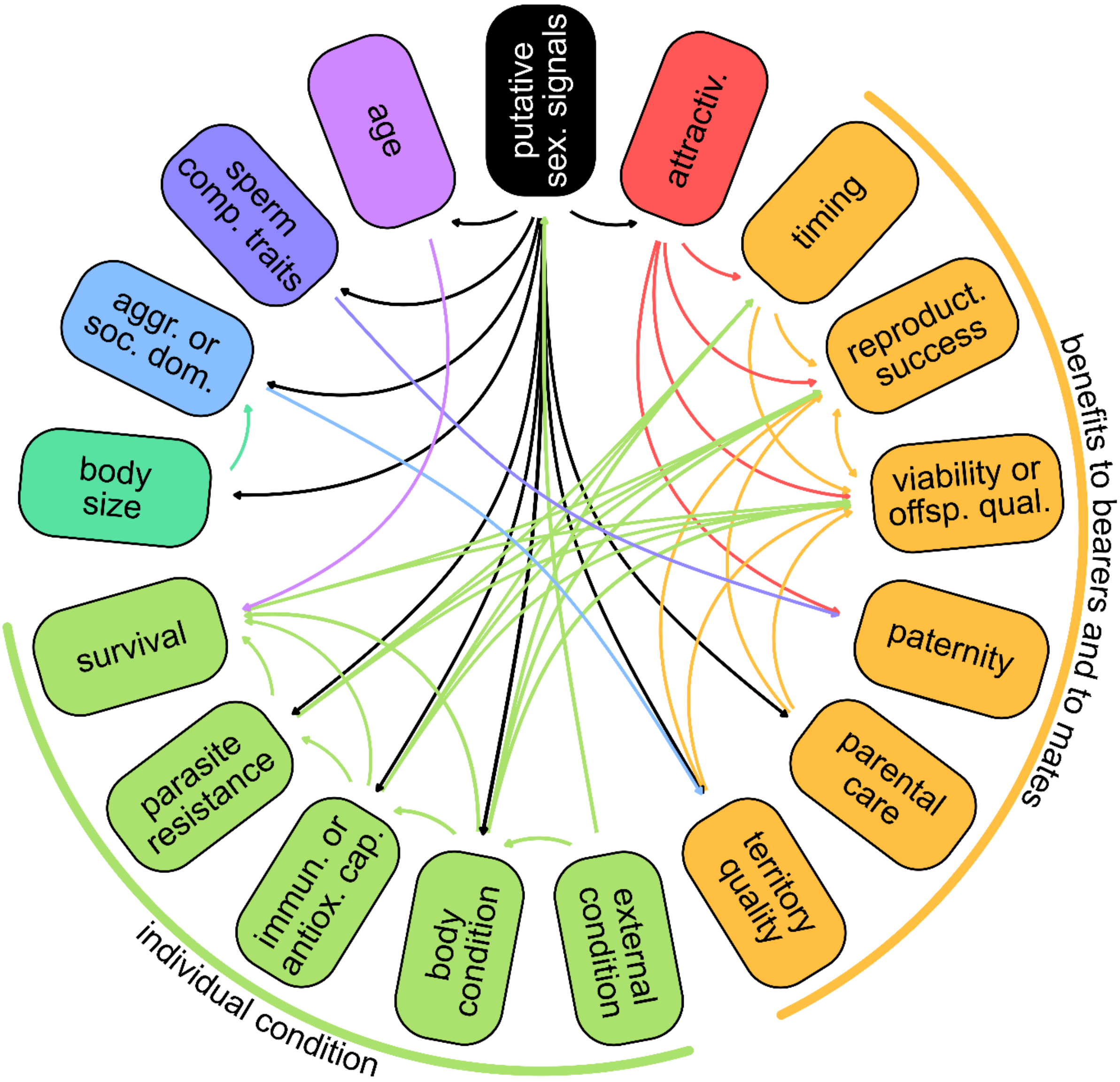

Figure 1.

Framework for the relationship between putative sexual signals and different variables (clockwise from the top): conspicuousness of putative sexual signals, attractiveness to prospective mates, benefits to signal bearers and to their 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 represent that a variable potentially influences or signals another variable (see text for details).

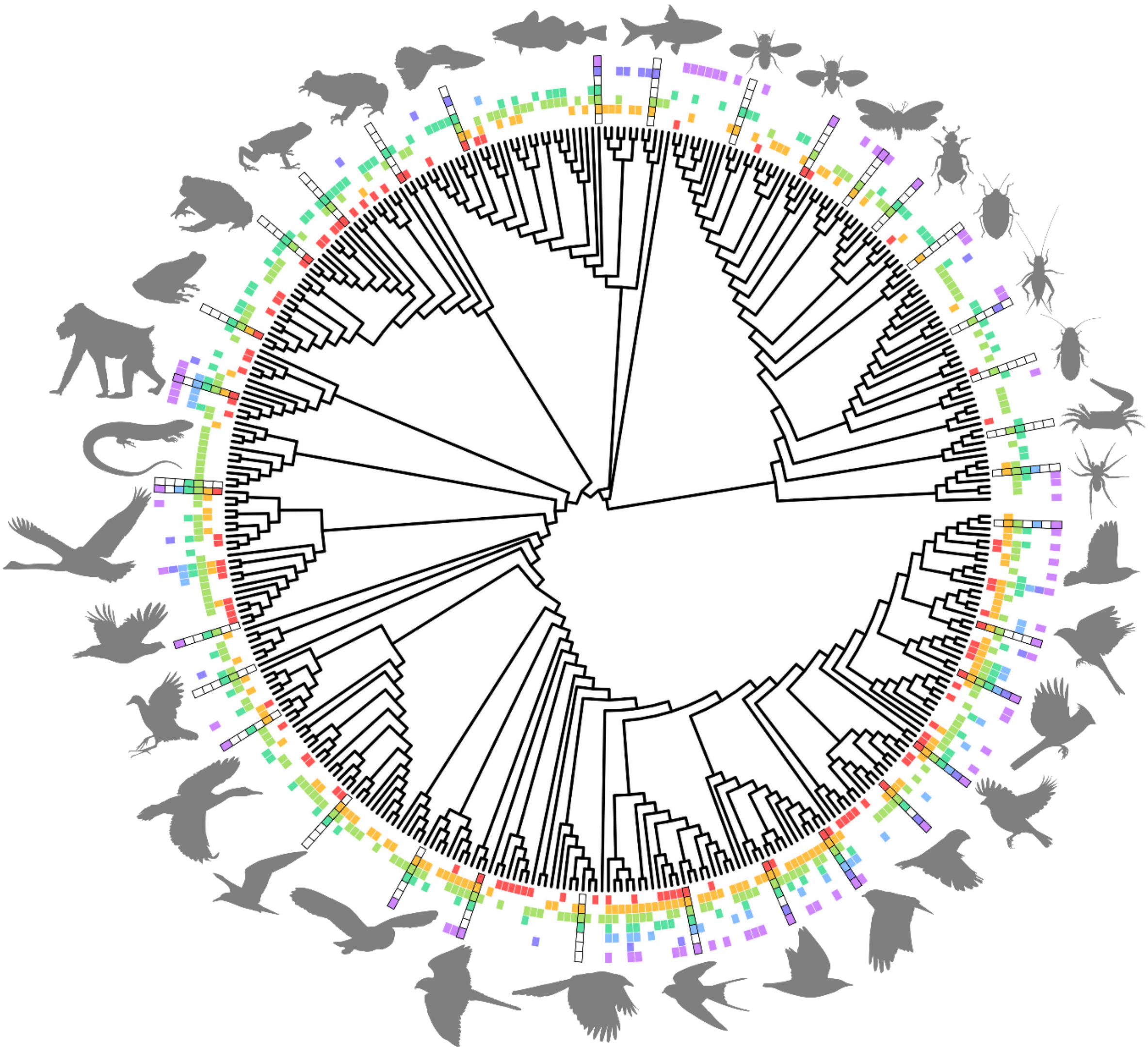

Figure 2.

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 to prospective mates, orange: benefits to signal bearers and to their 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.

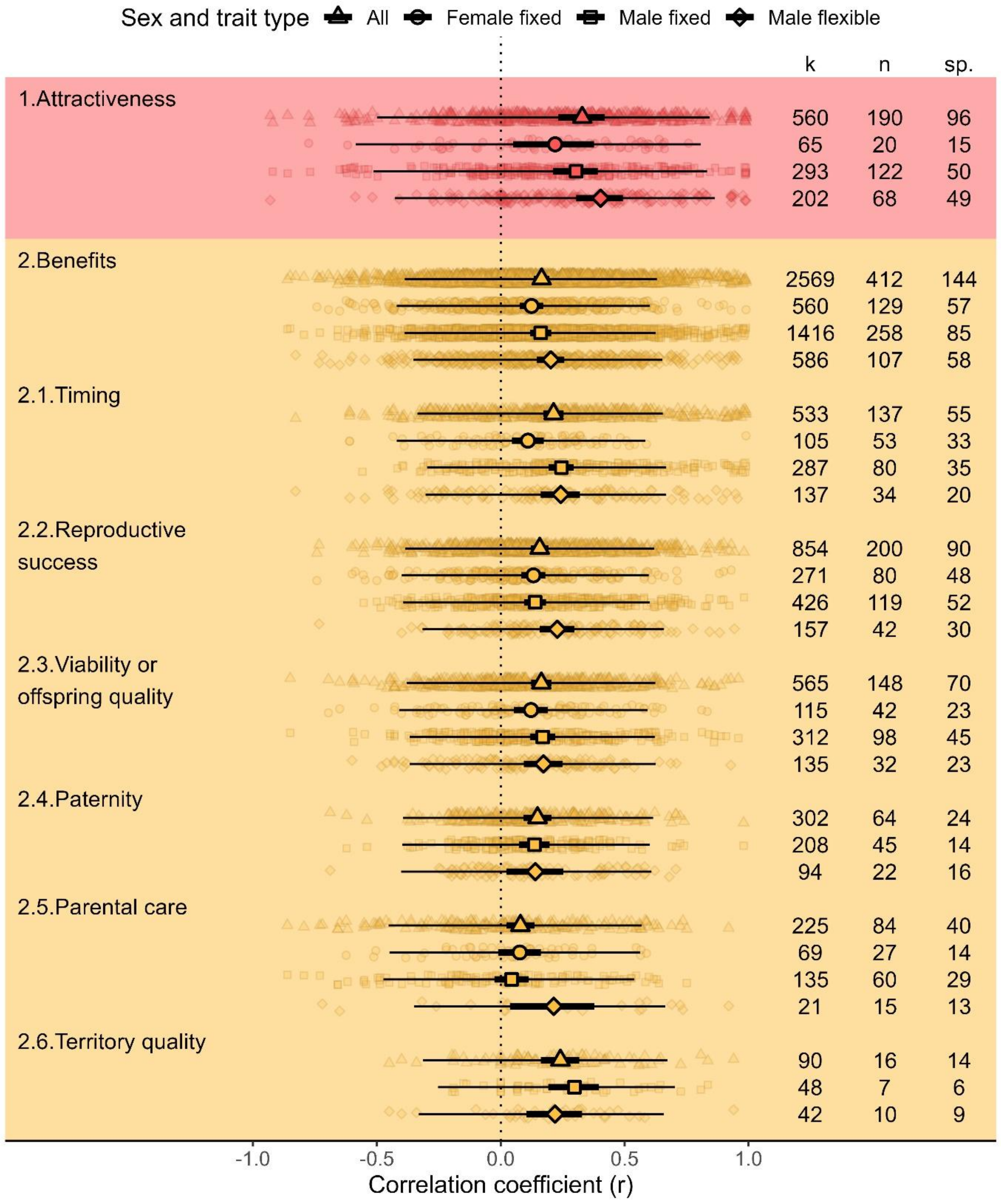

Figure 3.

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). Thick lines represent 95% confidence intervals while thin lines represent 95% predictive intervals. The vertical dotted line highlights zero (no relationship). k, n, and sp. represent, respectively, the number of effect sizes, empirical studies, and species for each set. The category “all” represents data regarding all trait types from all individuals (females, males, and unknown or mixed sex).

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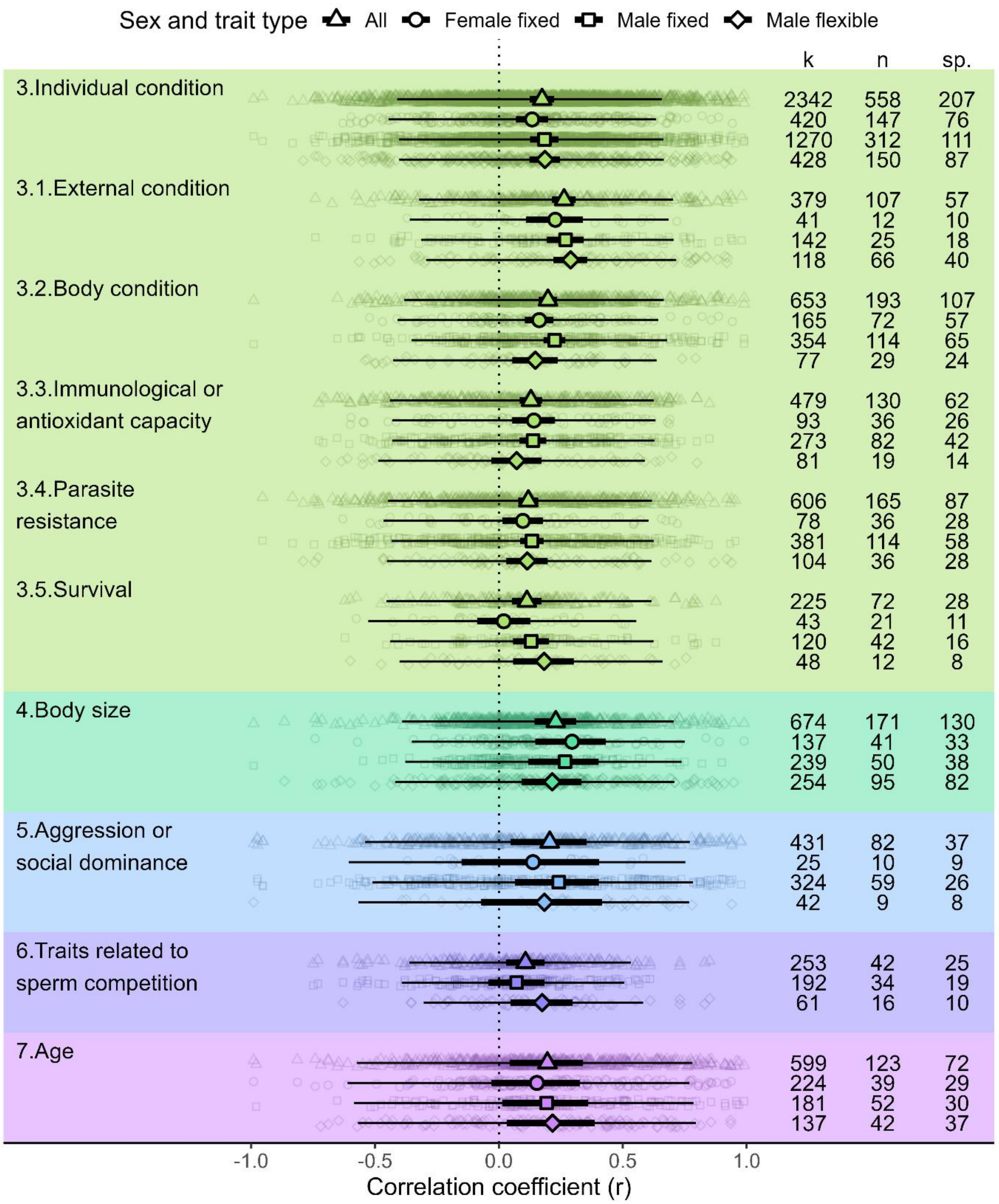

991

992 *Figure 4.*

993 Mean effect sizes for the relationship between the conspicuousness of putative sexual signals

994 and their bearers' condition, body size, aggression or social dominance, traits related to sperm

995 competition, or age. Variance explained by fixed factors in these models (marginal R^2) were,

respectively, 4.9%, 1.2%, 1.9%, 3.3%, and 0.5% (see Table S6). Thick lines represent 95% confidence intervals while thin lines represent 95% predictive intervals. The vertical dotted line highlights zero (no relationship). k, n, and sp. represent, respectively, the number of effect sizes, empirical studies, and species for each set. The category “all” represents data regarding all trait types from all individuals (females, males, and unknown or mixed sex).

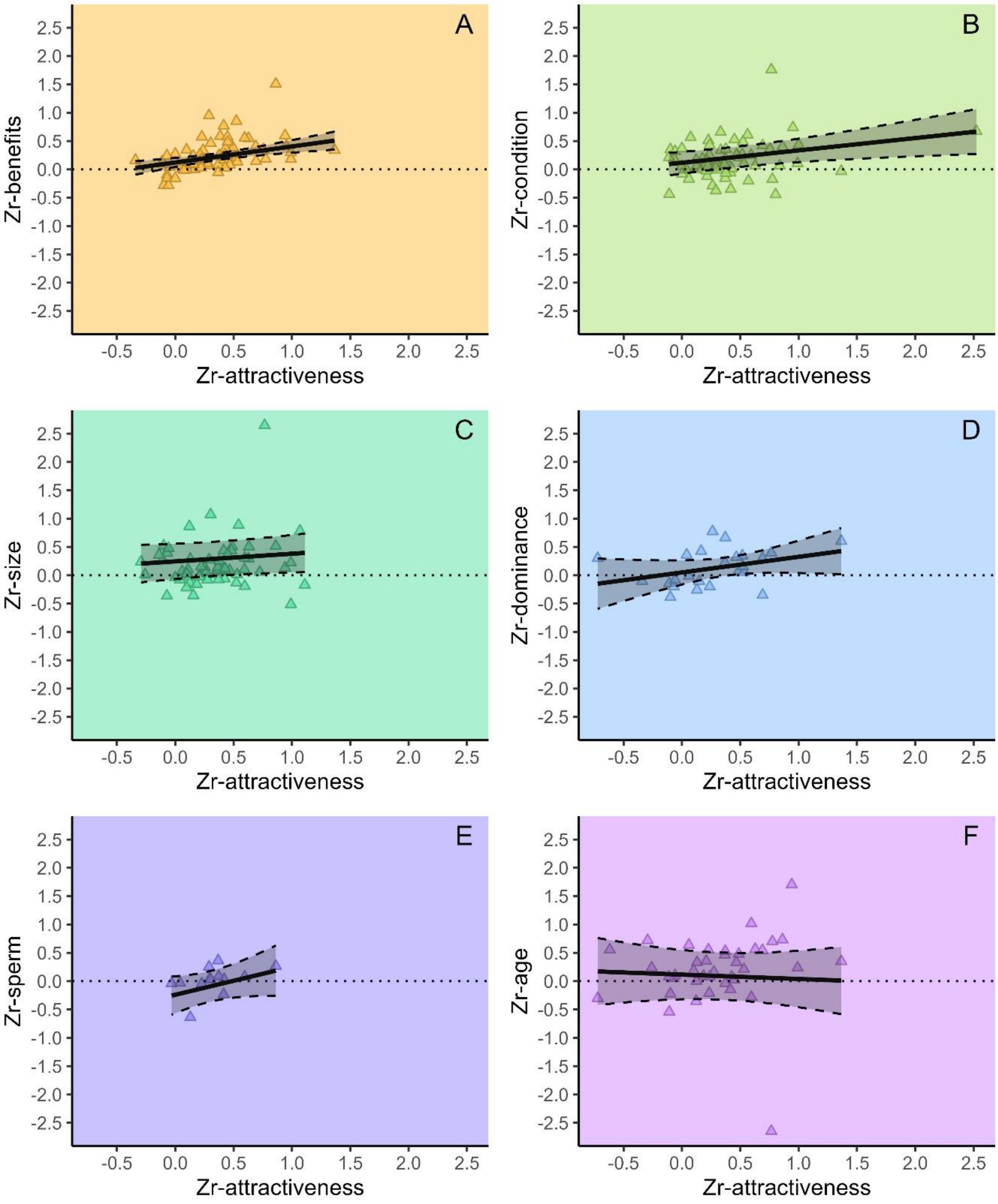

Figure 5.

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 competition, F: age). Solid lines represent slopes, hashed areas between dashed lines represent slopes’ 95% confidence interval, and dotted lines highlight zero.

Supplementary material

Appendix 1: Deviations from the pre-registration

PP 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 he decided against it because this variable overlapped with trait type (e.g. most fixed putative sexual signals were visual traits). PP 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 (Pollo *et al.* 2025). PP adjusted variables within our framework from our pre-registration (compare our Table S1 with Table 1 in Pollo *et al.* 2024b, see also Pollo *et al.* 2025).

Appendix 2: Empirical studies whose data we re-extracted

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Figures

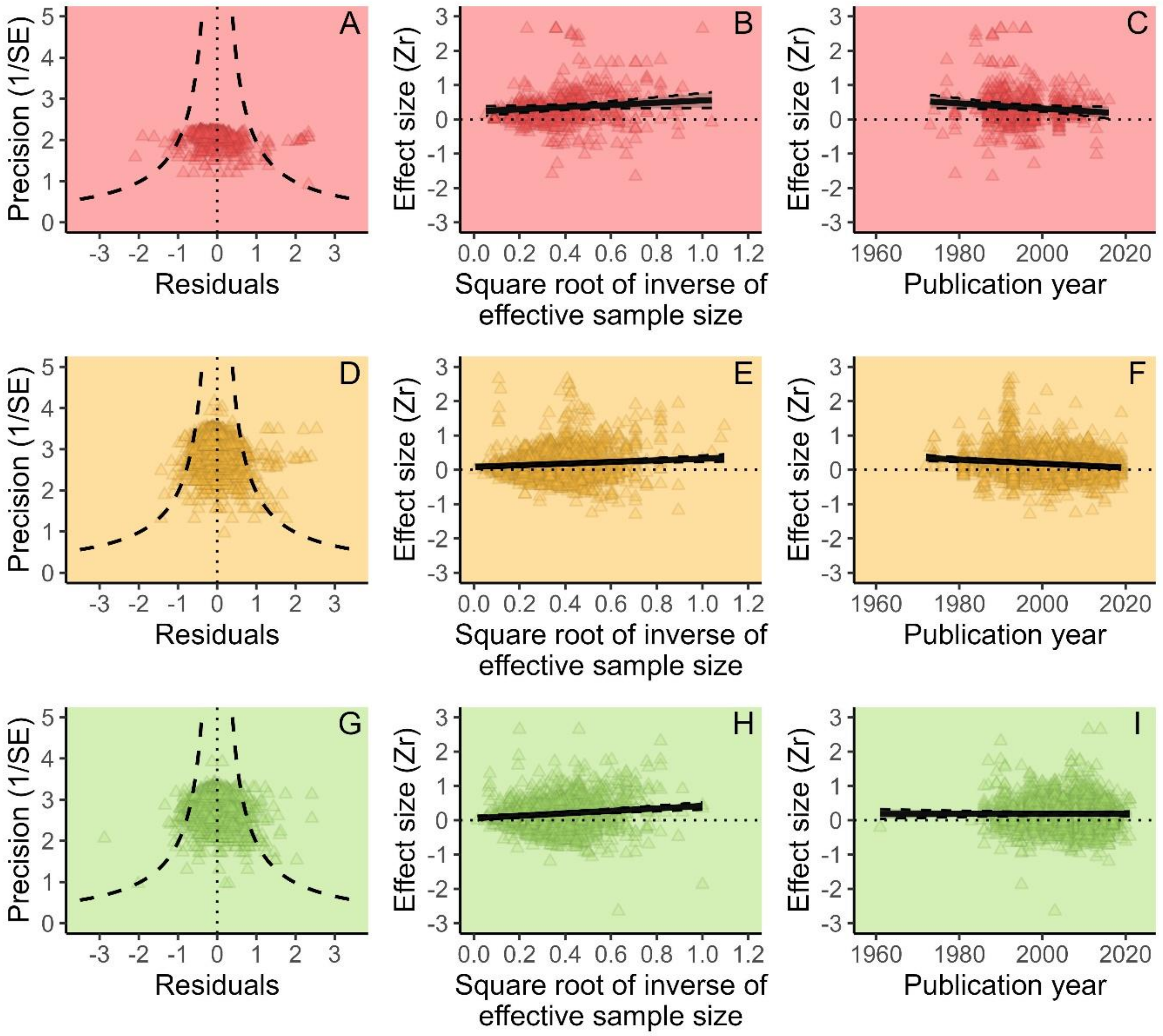

Figure S1.

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).

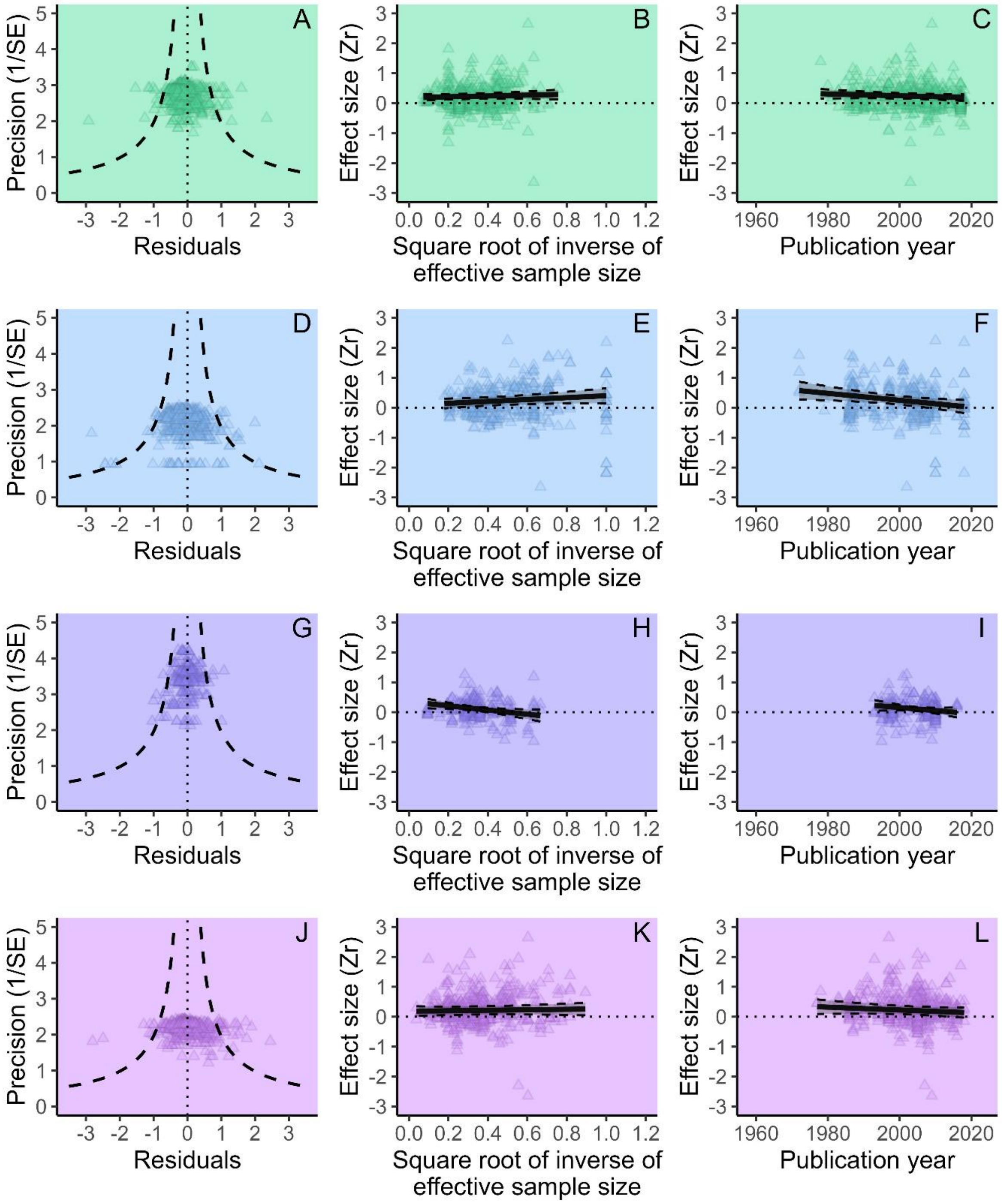

Figure S2.

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 values (A, D, G, J) or for regression estimates (B, C, E, F, H, I, K, L). Panels refer to body size (A-C), aggression or social dominance (D-F), traits related to sperm competition (G-I), or age (J-L).

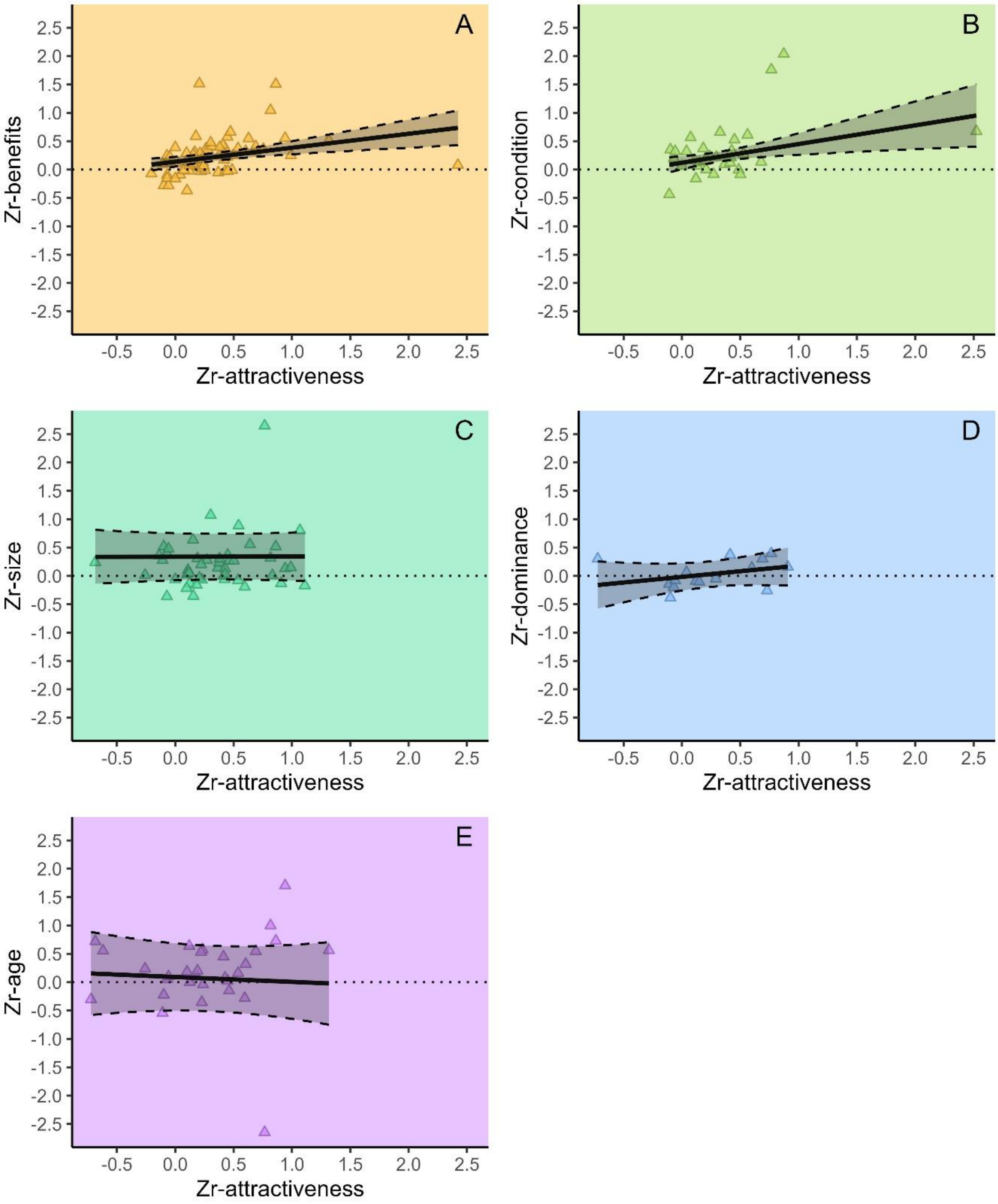

Figure S3.

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:

aggression of social dominance, E: age). Solid lines represent slopes, hashed areas between dashed lines represent slopes’ 95% confidence interval, and dotted lines highlight zero.

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).

<u>Figure S5.</u>

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).

Tables

Table S1.

Variables within our framework, for which we verified the relationship with putative sexual signal conspicuousness. *N* represents the number of primary meta-analyses in our dataset that explored these variables. Underlined examples are predicted to have a negative relationship with sexual signal conspicuousness, while others are predicted to have a positive relationship with sexual signal conspicuousness.

Variable	**Sub variable**	***N***	**Examples**
Attractiveness	-	15	Copulation success, harem size, success in mate choice trials, divorce, pairing success or status
Benefits to sexual signal bearers or to their mates	Timing	9	Latency to arrive at breeding site, latency to nest, latency to pair, latency to mate, latency to breed, latency to lay eggs, latency for eggs to hatch, latency for offspring to fledge
	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, cuckoldry occurrence
	Parental care	7	Feeding rate, incubation frequency
	Territory	2	Territory quality or size
Individual condition	External condition	7	Increase in brood size or reproductive effort, decrease in brood size or reproductive effort, habitat quality, mother's condition, date when reared, diet supplementation, dietary deprivation, nutritional stress
	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, glucocorticoids, hematocrit, heterophil-to-lymphocyte ratio, oxidative damage, white blood cells
	Parasite resistance	10	Abundance of parasites, infection with a pathogen, pathogen richness, 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, received aggression, dominance, fights initiated, social rank, nest defence, distance from intruder, 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)

Table S2.

Presumed directionality of conspicuousness among various putative sexual signals.

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

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

		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
Individual condition	-	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
	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

Table S4.

Heterogeneity measures observed in meta-analytical models on the relationship between the expression of putative sexual signals and different variables within our framework.

Heterogeneity measure	**Variable**	**Total**	**Within-study (effect size ID)**	**Across-study (study ID)**	**Across-species (species ID)**	**Phylogeny**	**Within-species trait type**
I^2	Attractiveness	91.512	56.518	26.204	0.087	2.416	6.288
	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	4.278	<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	<0.001
	Age	93.585	44.460	28.500	<0.001	7.395	13.230
CV	Attractiveness	1.745	1.078	0.500	0.002	0.046	0.120
	Benefits to sexual signal bearers or to their mates	3.094	1.814	0.881	0.024	<0.001	0.376
	Individual condition	3.126	1.924	0.978	0.175	0.048	<0.001
	Body size	1.947	0.783	0.096	<0.001	0.080	0.988
	Aggression or social dominance	3.814	0.966	2.095	0.454	0.254	0.044
	Traits related to sperm competition	5.132	2.148	2.905	<0.001	0.080	<0.001
	Age	4.620	2.195	1.407	<0.001	0.365	0.653
M	Attractiveness	0.636	0.393	0.182	0.001	0.017	0.044
	Benefits to sexual signal bearers or to their mates	0.756	0.443	0.215	0.006	<0.001	0.092
	Individual condition	0.758	0.466	0.237	0.043	0.012	<0.001
	Body size	0.661	0.266	0.032	<0.001	0.027	0.335
	Aggression or social dominance	0.792	0.201	0.435	0.094	0.053	0.009
	Traits related to sperm competition	0.837	0.350	0.474	<0.001	0.013	<0.001
	Age	0.822	0.391	0.250	<0.001	0.065	0.116

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

Table S6.

Marginal R^2 (i.e. variation of data explained by fixed factors) and conditional R^2 (i.e. variation of data explained by random and fixed factors) of meta-analytical models on the relationship between putative sexual signal conspicuousness and different variables, with sub variable, sex, and trait type as fixed factors.

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

Table S7.

Results of meta-analytical models on the relationship between putative sexual signal conspicuousness and different variables, with the square root of the inverse of effective sample size (SIESS) and publication year of empirical sources as moderators. Positive estimates for SIESS indicate publication bias and negative estimates for publication year indicate time-lag publication bias (shaded rows highlight these cases when statistically significant).

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

Table S8.

Association between the relationship between putative sexual signal conspicuousness and attractiveness (Zr-attractiveness) and the relationship between putative sexual signal conspicuousness and other variables (benefits: Zr-benefits, individual condition: Zr-condition, body size: Zr-size, aggression or social dominance: Zr-dominance, traits related to sperm competition: Zr-sperm, and age: Zr-age), depending on two approaches (across- and within-studies) and two distinct models (uni- and bivariate). *N* indicates the number of effect sizes used in each approach. Shaded rows highlight estimates whose 95% confidence interval does not overlap zero.

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